SHOUT
SHARE
IT

MVS
4890

HARVARD UNIVERSITY

Library of the
Museum of
Comparative Zoology

2194
1-2

BULLETIN

OF THE

MUSEUM OF COMPARATIVE ZOOLOGY

HARVARD UNIVERSITY

VOL. 131

CAMBRIDGE, MASS., U.S.A.
1964

The Cosmos Press, Inc.
Cambridge, Mass., U. S. A.

CONTENTS

PAGE

No. 1.—AMERICAN SPIDERS OF THE GENUS *Episinus* (ARANEAE: THERIDIIDAE). By Herbert W. Levi. March, 1964 1

No. 2.—FOSSIL MAMMALS FROM THE LOWER PLIOCENE OF FISH LAKE VALLEY, NEVADA. By John B. Clark, Mary R. Dawson and Albert E. Wood. March, 1964 27

No. 3.—AMERICAN SPIDERS OF THE GENUS *Phoroncidia* (ARANEAE: THERIDIIDAE). By Herbert W. Levi. April, 1964 65

No. 4.—THE BRAINCASE OF THE PALEOZOIC ELASMOBRANCH *Tamiobatis*. By Alfred Sherwood Romer. (1 Plate.) April, 1964 87

No. 5.—THE TAXONOMIC STATUS OF *Heptaxodon* AND DENTAL ONTOGENY IN *Elasmodontomys* AND *Amblyrhiza* (RODENTIA: CAVIOMORPHA). By Clayton E. Ray. May, 1964. 107

No. 6.—THE SKELETON OF THE LOWER CARBONIFEROUS LABYRINTHODONT *Pholidogaster pisciformis*. By Alfred Sherwood Romer. (1 Plate.) May, 1964 . 129

No. 7.—EARLY EVOLUTION OF THE DISSOROPHID AMPHIBIANS. By Robert L. Carroll. (2 Plates.) June, 1964 161

No. 8.—THE GENUS *Micrathena* (ARANEAE, ARANEIDAE) IN THE WEST INDIES. By Arthur M. Chickering. June, 1964 251

PAGE

No. 9.—Revised Generic Diagnoses of the Fossil Fishes *Megalichthys* and *Ectosteorhachis* (Family Osteolepidae). By Keith Stewart Thomson. (1 Plate.) July, 1964 283

No. 10.—The Comparative Anatomy of the Snout in Rhipidistian Fishes. By Keith Stewart Thomson. August, 1964 313

No. 11.—The Anoles (Sauria, Iguanidae) of the Guadeloupéen Archipelago. By James D. Lazell, Jr. September, 1964 359

No. 12.—*Anolis equestris* in Oriente Province, Cuba. By Albert Schwartz. (1 Plate.) September, 1964 . 403

No. 13.—The Lynx Spiders of North America, North of Mexico (Araneae: Oxyopidae). By Allen R. Brady. September, 1964 429

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 1

AMERICAN SPIDERS OF THE GENUS *EPISINUS* (ARANEAE: THERIDIIDAE)

By Herbert W. Levi

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
March 4, 1964

PUBLICATIONS ISSUED BY OR IN CONNECTION WITH THE

MUSEUM OF COMPARATIVE ZOOLOGY AT HARVARD COLLEGE

BULLETIN (octavo) 1863 — The current volume is Vol. 131.

BREVIORA (octavo) 1952 — No. 197 is current.

MEMOIRS (quarto) 1864–1938 — Publication was terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 41 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 28 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained from the Publications Office of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1, 4 and 6 are out of print; volumes 3, 5, 7, 9, and 15 are sold by the Museum, and future volumes will be published under Museum auspices.

The Proceedings of the First International Symposium on Natural Mammalian Hibernation edited by C. P. Lyman and A. R. Dawe is available as volume 124 of the Museum of Comparative Zoology Bulletin. Published in 1960, it consists of 26 papers and a general discussion, totalling 550 pages. Price $3.00 paper back, $4.50 cloth bound.

PUBLICATIONS OF THE BOSTON SOCIETY OF NATURAL HISTORY

The remaining stock of the scientific periodicals of the Boston Society of Natural History has been transferred to the Museum of Comparative Zoology for distribution. Prices for individual numbers may be had upon request.

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 1

AMERICAN SPIDERS OF THE GENUS *EPISINUS* (ARANEAE: THERIDIIDAE)

By Herbert W. Levi

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
March, 1964

Bull. Mus. Comp. Zool., Harvard Univ., 131(1):1-25, March, 1964

No. 1 — *American Spiders of the Genus* Episinus (*Araneae: Theridiidae*)

By HERBERT W. LEVI

Many species of *Episinus* are known from only a single specimen; most species are rare. Many species are small and similar, and the degree of sclerotization of the transparent epigyna is highly variable, making their study difficult. The smaller species described here were examined twice, once in 1960 and again with better optical equipment in 1962. Most types of Simon were examined in 1958 and again in 1962. In addition to the many similar, minute species, there are a number of larger ones, most quite distinct in structure and also of rare occurrence. The generic placement of these larger species is often uncertain because of their greater diversity in appearance.

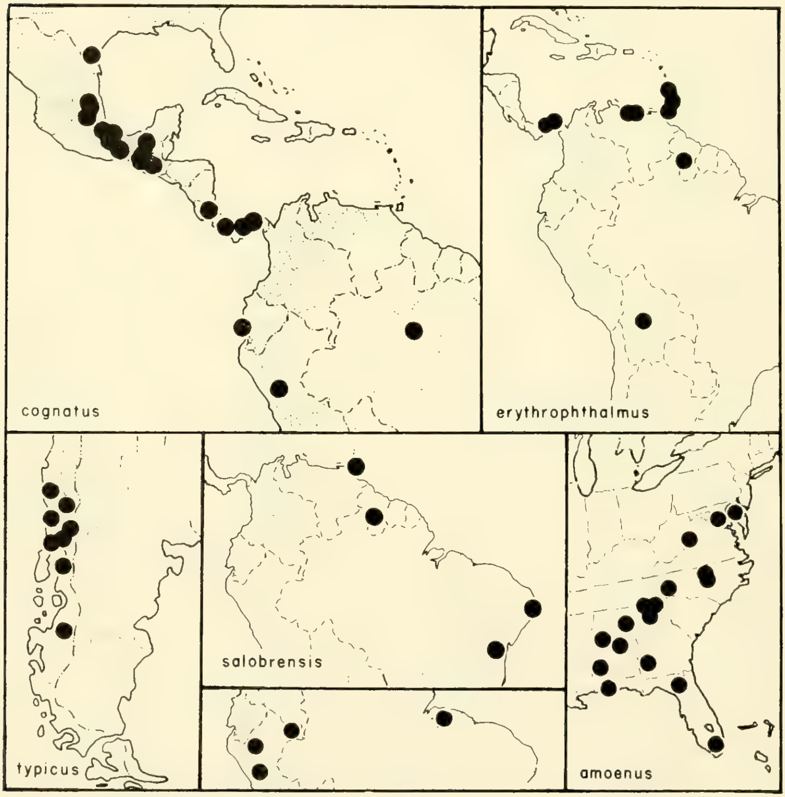
The study of American *Episinus* was made possible through the help of numerous colleagues who loaned collections and permitted me to examine types. I would like to acknowledge with thanks the loan of specimens from the following collections: Muséum National d'Histoire Naturelle, Paris (MNHN), by Prof. M. Vachon and J. F. Jézéquel; the American Museum of Natural History (AMNH) by Dr. W. J. Gertsch; the British Museum (Natural History) (BMNH) by Mr. D. J. Clark, Mr. K. H. Hyatt, Mr. E. Browning and Dr. G. Owen Evans; the personal collection of Prof. A. M. Chickering now housed in the Museum of Comparative Zoology; and personal collection of Mrs. D. Frizzell (Dr. H. Exline); the California Academy of Sciences (CAS) by Mrs. Frizzell and Dr. E. S. Ross; the Institut Royal des Sciences Naturelles de Belgique (ISNB) by Dr. A. Collart and Mr. J. Kekenbosch; the Senckenberg Museum (SMF) by Dr. O. Kraus; the Natural History Museum, Stockholm, by Dr. L. Brundin; the Naturhistorisches Museum, Vienna, by Dr. M. Beier, and specimens from Miss H. Zapfe (Mrs. G. Mann). I am grateful to Fr. Chrysanthus for checking the latinization of specific names. The examination of types in European museums was made possible by a National Science Foundation Grant (G-4317), the completion of the revision by a grant from the National Institutes of Health (AI-01944).

EPISINUS Latreille

Episinus Latreille, 1809, Genera Crustaceorum et Insectorum, 4: 371. Type species by monotypy *E. truncatus* Latreille, 1809, of Europe.

Carapace often with a pair of horns between anterior and posterior median eyes. Lenses of lateral and posterior median eyes often on tubercles, with silvery and sometimes reddish pigment. Chelicerae small with a tooth or teeth on anterior margin, sometimes without teeth. First legs longest. Abdomen usually modified with humps, tubercles, and sometimes with small nipples, often light-colored with gray marks, streaks and sometimes white pigment. The smaller species have less pigment than larger ones. Colulus replaced by two setae.

Palpus extremely complex, all structures proliferated, large, connected by large haematodocha.



Distribution of *Episinus cognatus*, *erythrophthalmus*, *typicus*, *salobrensis*, *immundus*, *amoenus*.

Species of *Episinus* are found in all parts of the world, although most occur in warmer regions. The distribution of the commonest American species is illustrated by the map.

Episinus has many species in tropical America. Most species are small with little pigment, the abdomen is subtriangular, and there is a pair of horns between the eyes. However, several species are larger, pigmented, and have the abdomen longer than wide. *Episinus cognatus*, the largest, has indications of horns between the eyes; *E. recifensis*, known only from the male and also large, has horns. The genitalia of males of the large species are similar to those of the smaller ones.

Episinus americanus Nicolet, 1849, *in* Gay, Historia de Chile, Zool., 10: 543 is probably an argiopid related to *Micrathena*.

Episinus brasilianus Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, 2(1): 206, pl. 10, fig. 124, ♀. Female holotype from Brazil in the Naturhistorisches Museum, Vienna, examined, is a female *E. truncatus* Latreille, a European species. Most likely the locality is in error.

In the keys, "Fig." capitalized refers to this paper, "fig." in lower case, to the previous paper (Levi, 1955, Jour. New York Ent. Soc., 62: 65-90).

Key to male *Episinus*

1a. Total length greater than 2.6 mm (carapace more than 1.0 mm wide) 2
1b. Total length less than 2.3 mm (carapace less than 0.9 mm wide) 5
2a. Length of palpal tibia about equals that of cymbium. 3
2b. Length of palpal tibia less than two thirds that of cymbium 4
3a. Conductor (at distal mesal tip) with hook (1955, fig. 8); Texas to Peru *cognatus*
3b. Conductor without such hook (Fig. 8); eastern Brazil .....*recifensis*
4a. Embolus base hidden by tegulum (1955, fig. 4); southeastern United States *amoenus*
4b. Embolus base visible in ventral view (Fig. 15); Chile ....*typicus*
5a. Total length greater than 1.8 mm; filiform portion of embolus of palpus with two bends, S-shaped (1955, fig. 13; Fig. 4) 6
5b. Total length less than 1.7 mm; filiform portion of palpus evenly curved 7
6a. Diameter of anterior median eyes more than three times that of other eyes; conductor as in Figure 4; Cuba, Hispaniola ....*gratiosus*
6b. Diameter of anterior median eyes less than twice that of other eyes; conductor as in 1955, figure 13; Panama to Guianas *bruneoviridis*
7a. Conductor tipped with an ectally directed spine (Fig. 78); Trinidad to eastern Brazil *salobrensis*

7b. Conductor otherwise 8

8a. Palpal tibia equal in length or longer than cymbium 9

8b. Palpal tibia less than two-thirds cymbial length 11

9a. Embolus filament a relatively thick, short structure (Fig. 57); southeastern Brazil *bicorniger*

9b. Embolus filament a relatively fine, long structure; Central America 10

10a. Distal margin of embolus base almost transverse to long axis of cymbium; distal portion of bulb with an ectal projection (Fig. 50); Nicaragua *aspus*

10b. Distal margin of embolus base not transverse, ectal projection lacking (1955, fig. 14); Panama *panamensis*

11a. Length of palpal tibia less than one-third cymbial length; palpal bulb tipped by two transparent projections (1955, fig. 11); Mexico to Panama *colima*

11b. Length of palpal tibia about equal to or more than half length of cymbium; bulbal tip otherwise 12

12a. Bulbal tip with a sclerotized elbowed piece (1955, fig. 12); Bahama Isls., Jamaica *nadleri*

12b. Bulbal tip otherwise 13

13a. Distal end of palpal bulb with an ectal pointing hook (Fig. 45); Panama *raticus*

13b. Distal end otherwise 14

14a. Embolus base with a mesally directed lobe above filiform portion (Figs. 90-93); Panama to Bolivia *erythrophthalmus*

14b. Embolus base without a mesally directed lobe above base of filiform portion (1955, figs. 5, 7); Mexico 15

15a. Ectal sclerotized margin of conductor widest on distal end (1955, fig. 5) *juarezi*

15b. Ectal sclerotized margin of conductor widest on proximal end (1955, fig. 7) *chiapensis*

Key to female *Episinus*

1a. Abdomen with a large dorsal extension, higher than long or wide (Fig. 24); southeastern Brazil *teresopolis*

1b. Abdomen otherwise with at most a median dorsal tubercle 2

2a. Abdomen widest anteriorly 3

2b. Abdomen widest in middle or posteriorly 4

3a. Abdomen with a median dorsal tubercle (Fig. 23); Venezuela *implexus*

3b. Abdomen without median dorsal tubercle (Fig. 11); Panama *emanus*

4a. Abdomen subspherical with a median dorsal tubercle (Figs. 30, 31); Peru *malachinus*

4b. Abdomen otherwise 5

5a. Abdomen longer than wide; total length more than 2.4 mm 6

5b. Abdomen as wide as long or wider than long or if longer than wide, total length less than 2.2 mm 10

6a. Abdomen with a dorsal distinct white folium pattern bordered by black (1955, fig. 34); Panama to Guianas *bruneoviridis*
6b. Abdomen otherwise 7
7a. Epigynum with an anterior sclerotized raised knob (Fig. 13); abdomen pointed anteriorly (Fig. 14); Chile [illegible]
7b. Epigynum otherwise; abdomen truncate anteriorly 8
8a. Epigynum with a slight depression bordered anteriorly and around sides (1955, fig. 21); total length more than 4.4 mm; Texas to Central Peru .... *cognatus*
8b. Epigynum depression not bordered anteriorly; total length less than 4.5 mm; eastern U. S. west to Alabama, Cuba, Hispaniola 9
9a. Epigynum depression anterior to seminal receptacles (Figs. 1, 2); Cuba, Hispaniola *gratiosus*
9b. Epigynum depression posterior to seminal receptacles (1955, fig. 17); eastern U. S., Maryland to Alabama *amoenus*
10a. Abdomen subspherical, widest in middle (Figs. 18, 20) or diamond-shaped (Fig. 7); total length 4.0 mm or more 11
10b. Abdomen subtriangular, widest near posterior; total length less than 3.0 mm 12
11a. Abdomen with humps on middle of sides (Fig. 7); epigynum with a scape (Fig. 6); seminal receptacles sausage-shaped; Peru *albostriatus*
11b. Abdomen without humps (Fig. 18) or humps posterior (Fig. 20); epigynum with a depression (Figs. 17, 22) [illegible]
12a. Abdomen with a median anterior tubercle (Fig. 54); Venezuela *bimucronatus*
12b. Abdomen without anterior tubercle 13
13a. Abdomen with dorsal tubercles or nipples 14
13b. Abdomen without dorsal tubercles or nipples 19
14a. Abdomen with a single median dorsal nipple (Fig. 37) 15
14b. Abdomen with several dorsal nipples (Figs. 27, 34, 40) 16
15a. Duct winding twice around seminal receptacles (1955, fig. 31); Mexico *putus*
15b. Duct winding once around seminal receptacles (Fig. 38); Panama *panamensis*
16a. Abdomen wider than long, lateral tubercles crowned by thorns (Fig. 27); epigynum with a small central depression (Fig. 29); Jamaica [illegible]
16b. Abdomen longer than wide or length equals width (Fig. 34); epigynum otherwise 17
17a. Epigynum with a distinct transverse lip (Fig. 36); Panama *pyrus*
17b. Epigynum otherwise 18
18a. Connecting ducts wound once around seminal receptacles (Fig. 41); Peru [illegible]
18b. Connecting ducts probably very short (1955, figs. 26, 27); Hispaniola [illegible]

19a. Epigynum depression with a median septum (Fig. 44); ducts short, opening into middle of ectal side of seminal receptacles (Fig. 43); Costa Rica, Panama ... *vaticus*

19b. Epigynum and ducts otherwise ... 20

20a. Epigynum openings in two dark spots anterior to seminal receptacles (Figs. 55, 56); southeastern Brazil ... *bicorniger*

20b. Epigynum openings otherwise ... 21

21a. Openings in a corner of a depression; area anterior and between seminal receptacles sclerotized (Fig. 66); eastern Brazil to Paraguay ... *nebulosus*

21b. Openings usually indistinct; area between seminal receptacles sometimes sclerotized but not anteriorly ... 22

22a. Seminal receptacles long and S-shaped (Figs. 73, 74); Trinidad to eastern Brazil ... *salobrensis*

22b. Seminal receptacles not S-shaped ... 23

23a. Duct coiling twice around receptacles (1955, fig. 31); Mexico ... *juarezi*

23b. Ducts coiling at most once around receptacles ... 24

24a. Seminal receptacles spherical (1955, fig. 29); Bahama Isls., Jamaica *nadleri*

24b. Seminal receptacles ovoid or longer than wide; Central America and South America ... 25

25a. Epigynum with a median anterior dark spot (Fig. 49); connecting ducts not coiled completely around seminal receptacles (Fig. 48); Nicaragua ... *aspus*

25b. Epigynum without median dark spot; connecting ducts coiled at least once around seminal receptacles ... 26

26a. Connecting ducts entering openings from posterior (Figs. 58-61); Venezuela ... *zurlus*

26b. Connecting ducts entering openings from side ... 27

27a. Dorsum of abdomen with a longitudinal dusky band and two cross bands (Fig. 72); median area of epigynum light (Fig. 71); Mato Grosso ... *bicruciatus*

27b. Dorsum of abdomen light, epigynum without such median light area (Figs. 81, 83, 85); Panama to Bolivia ... *erythrophthalmus*

EPISINUS IMMUNDUS (Keyserling), new combination
Figures 16-22, Map

Theridium immundum Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, 2(1): 89, pl. 4, fig. 57, ♀. Two female syntypes from Le Para [Belém, Pará], Brazil, in the Muséum National d'Histoire Naturelle, Paris, examined. Other syntypes come from Pebas, [Loreto], Peru.

Theridium bituberculatum Keyserling, 1884, *op. cit.*, 2(1): 92, pl. 4, fig. 60. Juvenile female holotype from Pevas, Amazonas, [Pebas, Loreto, Peru], in the Muséum National d'Histoire Naturelle, Paris, examined. NEW SYNONYMY.

Thymoites immundis, — Keyserling, 1886, *op. cit.*, 2(2): 295.
Thymoites bituberculatus, — Keyserling, 1886, *op. cit.*, 2(2): 295.
Thymoites bigibbosus Roewer, 1951, Abhandl. naturwiss. Verein Bremen, 32: 504. New name for *Thymoites bituberculatus* Keyserling, thought preoccupied by *Hypomma bituberculatus* Wider. NEW SYNONYMY.

Description. Carapace rich brown with some silvery reddish pigment between lateral eyes. Sternum light brown with dark brown spots; spots on sides emphasize the lobes (Fig. 19). Legs banded rich dark brown on light. Dorsum of abdomen gray with indistinct darker gray maculations; venter with some white pigment between epigastric groove and spinnerets. Eye region of carapace narrow, region between eyes swollen. Eyes subequal in size, anterior median eyes two-thirds diameter apart, almost touching laterals; posterior median eyes one diameter apart, in some specimens almost touching laterals. Chelicerae with two long teeth on anterior margin, none on posterior. Sternum with lobes on sides (Fig. 19). The abdomen is subspherical or with posterior humps (Figs. 18, 20). Total length of a syntype 5.2 mm. Carapace 2.3 mm long, 2.1 mm wide. First femur, 3.1 mm; patella and tibia, 3.2 mm; metatarsus, 1.4 mm; tarsus, 0.8 mm. Second patella and tibia, 2.7 mm; third, 1.9 mm; fourth, 2.6 mm.

Figures 16-19 were prepared from a syntype specimen from Belém, Brazil.

Note. The species is quite variable judging by the five specimens available. The posterior median eyes may be more or less close to the laterals. The humps of the abdomen may be almost missing (Fig. 18) or be distinct (Fig. 20). Both syntypes of *E. immundus* almost lack humps; the immature holotype of *T. bituberculatum* has humps. The epigynum depression may be surrounded by a lip (Fig. 17) or may have a lip only on sides and posterior (Fig. 22). One of the two syntypes from Belém has the depression bordered all around, the other one not. The internal genitalia may be so heavily sclerotized that the ducts are invisible, unless viewed from a lateral position, or they may be translucent.

The placement of this species in *Episinus* is not certain.

Distribution. Amazon Valley.

Records. Peru. San Martín: Mishqui-yacu, 20 km NE of Moyobamba, Aug. 1947, 2 ♀ (F. Woytkowski, AMNH). *Huanuco:* Cucharas, Huallaga Valley, Feb.-April 1954, ♀ (F. Woytkowski).

EPISINUS TYPICUS (Nicolet), new combination

Figures 12-15, Map

Theridion typicum Nicolet, 1849, *in* Gay, Historia de Chile, 3: 539. Type from Valdivia, Chile, lost.

? *Theridion agreste* Nicolet, 1849, *op. cit.*, p. 540. Type from Chile, lost.

Episinus dusenii Tullgren, 1902, Bih. Svensk. Vet. Ak. Handl., 28: 14, pl. 1, fig. 4, ♀. Female holotype from upper part of Aysen Valley, [Aysen], southern Chile in the Naturhistoriska Riksmuseet, Stockholm, examined. NEW SYNONYMY.

Note. This species usually has a pear-shaped abdomen (Fig. 14), described by Nicolet for two species. The small size in Nicolet's descriptions may indicate that he had immature specimens.

Description. Carapace yellow-brown, dark brown or gray on each side. Sternum yellow, darker on sides. Legs yellow-brown with dark brown bands as wide as intermediate areas. Abdomen mottled, black and white pigment above and with white pigment spots on sides; venter gray sometimes without pigment. Carapace highest in thoracic region with a longitudinal very distinct thoracic depression. Eyes subequal in size in female; posterior medians slightly larger than others in male. Anterior median eyes more than their diameter apart, almost touching laterals. Posterior medians their radius apart and their radius from laterals. Abdomen usually pear-shaped (Fig. 14), but quite variable. Anterior point of abdomen overhanging carapace. Colulus larger than usual in the genus, almost length of setae. Total length of female 3.5 mm. Carapace 1.4 mm long, 1.2 mm wide. First femur, 1.7 mm; patella and tibia, 1.8 mm; metatarsus, 1.9 mm; tarsus, 0.6 mm. Second patella and tibia, 1.2 mm; third, 0.9 mm; fourth, 1.8 mm. Total length of male 2.9 mm. Carapace 1.3 mm long, 1.1 mm wide. First femur, 2.0 mm; patella and tibia, 2.2 mm; metatarsus, 2.8 mm; tarsus, 1.0 mm. Second patella and tibia, 1.2 mm; third, 1.1 mm; fourth, 2.0 mm.

The epigynum has a central opening (Fig. 13). Anterior to the opening is a raised boss. The internal genitalia are heavily sclerotized (Fig. 12). The ectal margin of the palpal cymbium is lobed (Fig. 15).

Records. Chile. Arauco: Peillén – Pille, Cord. Nahualbuta, Jan. 1954 (L. Peña, ISNB); Pichinahuel, Cord. Nahualbuta, Dec. 1958 (L. Peña, ISNB). *Cautín:* Dalcahue, Feb. 1954, ♀ (L. Peña, ISNB). *Osorno:* 10 km E of Puyehue, 24 Jan. 1954 (E. S. Ross, A. E. Michelbacher, CAS); La Picada en el Volcán Osorno, Jan. 1958, ♀ (H. Zapfe); Río Gol-Gol, Feb. 1957, ♂

(L. Peña, ISNB). *Llanquihue:* Carelmapu, 27-28 Feb. 1957, ♀, ♂ (L. Peña, ISNB). *Chiloe:* Chaitén, 6 Feb. 1954 (L. Peña, ISNB).

EPISINUS BRUNEOVIRIDIS (Mello-Leitão)

Faiditus bruneoviridis Mello-Leitão, 1948, An. Acad. Brasileira Cienc., 20: 156, figs. 4, 5, ♀. Female holotype from Cane Grove, British Guiana in the British Museum, examined.

Episinus bruneoviridis, — Levi, 1955, Jour. New York Ent. Soc., 62: 70, figs. 13, 19, 20, 34, ♀, ♂.

This species is readily distinguished by the striking markings: a dorsal white folium on the long pear-shaped abdomen.

Distribution. Panama, Trinidad to Guianas.

Additional records. Panama Canal Zone: Barro Colorado Isl. (many collections); Summit; Forest Reserve; Chilibre; Fort Randolph (all A. M. Chickering).

EPISINUS EMANUS sp. n.

Figures 9-11

Type. Female holotype from Barro Colorado Island, Panama Canal Zone, June-July 1934 (A. M. Chickering), in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Description. Carapace yellow-brown; area between eyes white. Legs yellow, abdomen yellowish gray with a transverse line of white pigment spots between humps and an indistinct longitudinal median dorsal band of black pigment. Anterior median eyes slightly smaller than others; their diameter apart, slightly less than one-quarter diameter from laterals. Posterior eyes two-thirds diameter apart. Chelicerae without teeth. Fourth legs slightly longer than first. Abdomen subtriangular, widest anteriorly; with two tubercles (Fig. 11). Total length, 3.2 mm. Carapace, 1.2 mm long, 1.2 mm wide. First patella and tibia, 2.0 mm; second, 1.4 mm; third, 1.0 mm. Fourth femur, 2.1 mm; patella and tibia, 2.1 mm; metatarsus, 2.0 mm; tarsus 0.8 mm.

The specimen is in a poor state of preservation. Thus, the coloration of the abdomen is not distinct. The species probably belongs to *Episinus*. The area between the eyes is white as in some other members of the genus.

Diagnosis. The shape of the abdomen (Fig. 11) separates the species from *E. albostriatus*, and by the sclerotized internal genitalia (Fig. 9) it is readily separated from most other *Episinus* known.

EPISINUS ALBOSTRIATUS (Simon), new combination
Figures 5-7

Episinopsis albostriatus Simon, 1895, Ann. Soc. ent. France, 64: 136. Female holotype from Pebas, [Loreto], Peru, in the Muséum National d'Histoire Naturelle, Paris, examined.

Description. Carapace brown, region between eyes lightest. Sternum, legs brown. Abdomen with dark gray blotches on dorsum; venter mostly gray. Short horns between eyes. Eyes about subequal in size; laterals on slight tubercles. Anterior median eyes less than one diameter apart, almost touching laterals. Posterior median eyes less than one diameter apart; less than one diameter from laterals. Abdomen about as wide as long; a hump on each side (Fig. 7). Epigynum with a short scape (Fig. 6). Total length 4.2 mm. Carapace 1.6 mm wide, 1.4 mm long. First femur, 2.4 mm; patella and tibia, 2.5 mm; metatarsus, 2.6 mm. Second patella and tibia, 1.7 mm; third, 1.3 mm; fourth, 2.3 mm.

EPISINUS RECIFENSIS sp. n.
Figure 8

Type. Male holotype from Recife, Pernambuco, Brazil, in the Senckenberg Museum (no. RII /6323/1). The species is named after the type locality.

Description. Carapace yellow, white between eyes, some gray on sides and a narrow gray line around margin. Sternum, legs yellow. Abdomen whitish with a pair of long gray streaks anteriorly on dorsum and four pairs of gray spots posteriorly; whitish above spinnerets, which are surrounded by gray. Venter of abdomen mostly white. Carapace with two swollen horns between eyes, which are white. Anterior median eyes larger than posterior medians, much larger than anterior lateral eyes, almost twice their diameter. Anterior median eyes one-third their diameter apart, touching laterals. Posterior eyes their radius apart. Abdomen 1.6 times longer than wide, oval in shape. There are no indications of humps on the abdomen of the male. Total length 3.3 mm. Carapace 1.0 mm long, 1.0 mm wide. First femur, 2.5 mm; patella and tibia, 2.9 mm; metatarsus, 2.8 mm; tarsus, 1.0 mm. Second patella and tibia, 1.6 mm; third, 1.1 mm; fourth, 2.3 mm.

Diagnosis. The palpal tip (Fig. 8) and longer eye horns separate this species from *E. cognatus*.

Episinus cognatus O. P.-Cambridge

Map

? *Episinus longipes* Keyserling, 1884, Die Spinnen Amerikas, Theridiidae, 2 (1): 207, pl. 10, fig. 125, ♀, ♂. Male and female syntypes from Monterico, [900 m elev., Ayacucho, prov. Huanta], Peru, in the Polish Academy of Sciences, Warsaw, apparently lost. DOUBTFUL SYNONYMY.

Episinus cognatus O. P.-Cambridge, 1893, Biologia Centrali-Americana, Araneidea, 1: 109, p. 15, fig. 2, ♂. Male holotype from Teapa, [Tabasco], Mexico, in the British Museum. — Levi, 1955, Jour. New York Ent. Soc., 62: 71, figs. 8-10, 21, 22, 33, 41, ♀, ♂.

Episinopsis simplifrons Simon, 1897, Proc. Zool. Soc. London, p. 860. Juvenile holotype from St. Vincent Isl., Lesser Antilles, in the British Museum, examined. NEW SYNONYMY.

Note. Keyserling's 1884 description fits this species. His specimen was slightly larger than the ones I have examined. The illustrations match this species, although the epigynum of the Keyserling specimen seems to have been covered by secretion, as is common in this species. Unfortunately the type is lost, and thus the synonymy remains uncertain.

The central sclerotized area of the epigynal depression is larger and the depressed area has a slightly different shape in Peruvian specimens.

Distribution. Texas to Central Peru, Amazon (Map).

Additional records. Costa Rica. San José (E. Schmidt, AMNH). *Panama:* El Valle (A. M. Chickering). *Panama Canal Zone.* Barro Colorado Isl. (many collections); Summit (A. M. Chickering); Experimental Gardens (A. M. Chickering). *Ecuador. Guayas:* Colonche, 1941 (R. W. Landes); Milagro, Jan. 1943, juv. ♂ (H. E., D. L. Frizzell). *Peru. Huánuco:* Tingo María, Oct. 1946, ♀, Dec. 1946, ♂ (J. C. Pallister, AMNH); Oct. 1954 (E. I. Schlinger, E. S. Ross, CAS). *Brazil. Amazonas:* Manaus, Sept. 1962, ♀ (W. L. Brown).

Episinus gratiosus Bryant

Figures 1-4

Episinus gratiosus Bryant, 1940, Bull. Mus. Comp. Zool., 86: 313, fig. 65, ♀. Female holotype from Pico Turquino, 500 m, Oriente, Cuba, in the Museum of Comparative Zoology, examined.

Meotipa clementina, — Bryant, 1940, *ibid.*, 86: 314, figs. 79, 80, ♂. Not *M. clementinae* Petrunkevitch.

Description. Carapace, sternum yellow-brown with some darker marks. Legs yellow-brown with darker brown bands.

Abdomen with white pigment spots on dorsum, densest between tubercles. Sides of abdomen slightly darker, venter gray. Diameter of anterior median eyes larger than that of other eyes. Anterior median eyes of female one and one-half diameters apart, almost touching laterals; posterior median eyes one and one-half diameters apart, one diameter from laterals. Anterior median eyes of male one diameter apart almost touching laterals; posterior median eyes two diameters apart, one and one-half diameters from laterals. The abdomen is longer than wide (Fig. 3). There are two tubercles, one on each side, close to the posterior end. Total length of female 3.2 mm. Carapace 1.0 mm long, 0.9 mm wide. First femur, 1.8 mm; patella and tibia, 1.9 mm; metatarsus, 1.9 mm; tarsus, 0.5 mm. Second patella and tibia, 1.1 mm; third, 0.8 mm; fourth, 1.7 mm. Total length of male 2.2 mm. Carapace 0.94 mm long, 0.89 mm wide. First femur, 2.22 mm; patella and tibia, 2.24 mm; metatarsus, 2.31 mm; tarsus, 0.73 mm. Second patella and tibia, 1.07 mm; third, 0.81 mm; fourth, 1.82 mm.

Records. Cuba. Las Villas: Soledad, April 1936, ♂ (P. J. Darlington). Oriente: S. side Pico Turquino, 1100 m, June 1936, ♀ (P. J. Darlington). *Haiti.* Hills near Port-au-Prince, 600 m, 2 Oct. 1934, ♀ (P. J. Darlington).

EPISINUS AMOENUS Banks

Map

Episinus amoenus Banks, 1911, Proc. Acad. Nat. Sci. Philadelphia, 63: 445, figs. 13, 15. Male and female syntypes from the Swananoa River, North Carolina, in the Museum of Comparative Zoology, examined. — Levi, 1955, Jour. New York Ent. Soc., 62: 68, figs. 4, 17, 18, 32, 39, ♀, ♂.

Distribution. Eastern United States from Maryland to Florida and Alabama.

EPISINUS MALACHINUS (Simon), new combination

Figures 30-33

Janulus malachinus Simon, 1895, Ann. Soc. ent. France, 64: 135. Two female syntypes from Pebas, [Loreto], Peru, in the Muséum National d'Histoire Naturelle, Paris, examined.

Description. The specimens, almost colorless, are yellowish white in alcohol except for slight pigment behind anterior median eyes, some silvery spots around other eyes, and some white pigment spots on dorsum and posterior of abdomen. Eye region with two large horns. Eyes on tubercles, lens of anterior median eyes larger than that of others. Abdomen subspherical with a median dorsal tubercle (Figs. 30, 31). Total length 2.1 mm. Carapace 0.68 mm long, 0.61 mm wide. First femur, 1.58 mm; patella and tibia, 1.52 mm; metatarsus, 1.48 mm; tarsus, 0.56 mm. Second patella and tibia, 0.80 mm; third, 0.56 mm; fourth, 1.08 mm.

EPISINUS TERESOPOLIS sp. n.

Figures 24-26

Type. Female holotype, from Teresópolis, Est. Rio de Janeiro, Brazil, March 1946 (H. Sick), in the American Museum of Natural History. The specific name is a noun in apposition after the type locality.

Description. Carapace yellowish-white with a reddish spot on clypeus. Sternum, legs yellow-white. Abdomen with white pigment spots on dorsum and a red spot on each side. Eyes subequal in size. Anterior median eyes one diameter apart. Posterior median eyes one diameter apart, almost touching laterals. Horns between eyes. Abdomen with a dorsal projection (Fig. 24). Total length 1.5 m. Carapace 0.60 mm long, 0.52 mm wide. First femur, 0.98 mm; patella and tibia, 1.01 mm; metatarsus, 0.70 mm; tarsus, 0.43 mm. Second patella and tibia, 0.73 mm; third, 0.50 mm; fourth, 0.78 mm.

Diagnosis. Episinus teresopolis may be the same as *E. implexus* known only from an immature specimen from Venezuela. Both have a dorsal extension on the abdomen by which they differ from all other *Episinus* species.

Records. One ♀ paratype collected with type.

EPISINUS IMPLEXUS (Simon)

Figure 23

Hyocrea implexa Simon, 1894, Histoire Naturelle des Araignées, 1: 559; 1895, Ann. Soc. ent. France, 64: 146. Juvenile holotype from San Esteban, [Aragua], Venezuela, in the Muséum National d'Histoire Naturelle, Paris, examined.

The type examined is a juvenile and cannot be placed, although the abdomen shape (Fig. 23) may be diagnostic.

EPISINUS DOMINICUS Levi

Episinus dominicus Levi, 1955, Jour. New York Ent. Soc., 62: 77, figs. 26, 27, 38, ♀. Female holotype from Valle de Polo, Dominican Republic, in the American Museum of Natural History.

Distribution. Known from only the type specimen from Hispaniola.

EPISINUS UNITUS sp. n.
Figures 27-29

Type. Female holotype, from 3 km south of Unity Valley, St. Ann Parish, Jamaica, 9 Dec. 1954 (A. M. Nadler), in the American Museum of Natural History. The specific name is an arbitrary combination of letters.

Description. Carapace gray with a lighter V-shaped mark; eyes reddish. Sternum gray. Legs yellow-white. Abdomen gray with some white spots on sides; venter lighter with a reddish cast. Anterior median eyes larger than others, less than one diameter apart, almost touching laterals. Posterior median eyes one diameter apart, touching laterals. Horns between eyes. Abdomen with seven dorsal nipples in a transverse row (Fig. 27). Total length 1.4 mm. Carapace 0.65 mm long, 0.60 mm wide. First femur, 1.17 mm; patella and tibia, 1.27 mm; metatarsus, 1.17 mm. Second patella and tibia, 0.80 mm; third, 0.52 mm; fourth, 0.91 mm.

Diagnosis. Like *E. moyobamba*, *E. pyrus* and *E. dominicus*, the abdomen has numerous nipples (Fig. 27). The small distinct median depression of the epigynum (Fig. 29) and the shape of the seminal receptacles (Fig. 28) separate the species.

Record. One ♀ and juvenile paratypes collected with type.

EPISINUS MOYOBAMBA sp. n.
Figures 40-42

Type. Female holotype from Moyobamba, San Martín, Peru, 20 Dec. 1946 (J. C. Pallister), in the American Museum of Natural History. The specific name is a noun in apposition after the type locality.

Description. Carapace, sternum, legs yellow-white. Reddish around eyes. Ends of fourth femora and patellae slightly reddish. Abdomen with irregular gray marks, reddish around nipples, on each lateral projection and on posterior. Anterior median eyes larger than others, their diameter apart, almost touching laterals. Posterior median eyes three-quarters diameter apart, one-quarter from laterals. A pair of horns between eyes. Abdomen subtriangular with numerous dorsal nipples (Fig. 40). Total length 1.3 mm. Carapace 0.52 mm long. First femur, 1.00 mm. Second patella and tibia, 0.70 mm; third, 0.47 mm; fourth, 0.75 mm. (The specimen described is damaged.)

Diagnosis. Like the related *E. dominicus* the abdomen has nipples on the dorsum (Fig. 40). The connecting ducts wind once around the seminal receptacles (Fig. 41), while those of *E. dominicus* are shorter and do not wind around.

EPISINUS PYRUS sp. n.

Figures 34-36

Type. Female holotype from Summit, Panama Canal Zone, 16-17 August 1950 (A. M. Chickering), in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Description. Carapace yellow-white with a bright red median band (Fig. 34). Sternum yellow-white, legs yellow-white with distal end of femora and patellae dusky. Dorsum of abdomen mottled black but area around each nipple and lateral extension bright red (Fig. 34). A red patch on each side of abdomen. Venter yellow-white. Carapace with two horns between anterior median eyes. Anterior median eyes slightly larger than posterior medians, much larger than laterals, laterals on tubercles. Anterior median eyes three-quarters diameter apart. Posterior median eyes one diameter apart, their radius from laterals. Total length 1.2 mm. Carapace 0.52 mm long, 0.52 mm wide. First femur, 0.96 mm; patella and tibia, 1.08 mm; metatarsus, 0.71 mm; tarsus, 0.47 mm. Second patella and tibia, 0.62 mm; third, 0.47 mm; fourth, 0.78 mm.

Diagnosis. Like *E. dominicus* and *E. moyobamba* the abdomen has dorsal nipples (Fig. 34). The transverse lip of the epigynum (Fig. 36) separates *E. pyrus* from these related species. The connecting ducts are very short (Fig. 35).

Records. Panama Canal Zone: Summit Park, Dec. 1957, ♀ paratype (A. M. Chickering); Summit, 21-29 July 1950, ♀ paratype (A. M. Chickering).

EPISINUS COLIMA Levi

Episinus colima Levi, 1955, Jour. New York Ent. Soc., 62: 76, figs. 11, 40, ♂. Male holotype from Las Humedades, Armeria, Colima, Mexico, in the American Museum of Natural History.

The abdomen, which is missing from the holotype specimen, has a narrow ring of black broken by red around the edge of the dorsum. The large tubercle in the center is red with a black spot anteriorly. Otherwise the color is yellow-white. It is of the same shape as related species.

Distribution. Colima, Mexico, to Panama Canal Zone.

Records. Panama Canal Zone: Barro Colorado Isl., 20 April, 1953, ♂ (A. M. Nadler, AMNH).

EPISINUS PANAMENSIS Levi

Figures 37-39

Episinus panamensis Levi, 1955, Jour. New York Ent. Soc., 62: 73, figs. 14, 35, ♂. Male holotype, from Barro Colorado Island, Panama Canal Zone, in the American Museum of Natural History.

Description. Female pattern and coloration and general structure like that of male. The abdomen has one median dorsal nipple (Fig. 37). Total length 1.9 mm. Carapace 0.72 mm long, 0.65 mm wide. First femur, 1.62 mm; patella and tibia, 1.72 mm; metatarsus, 1.59 mm; tarsus, 0.60 mm. Second patella and tibia, 0.98 mm; third, 0.68 mm; fourth, 1.21 mm.

Record. Panama Canal Zone: Barro Colorado Island (numerous records).

EPISINUS VATICUS sp. n.

Figures 43-47

Type. Male holotype from Forest Reserve, Panama Canal Zone, 4-6 July 1939 (A. M. Chickering), in the Museum of Comparative Zoology. The specific name is an arbitrary combination of letters.

Description. Carapace yellow with a dusky line. Sternum gray. Legs yellow with some dusky marks. Dorsum of abdomen with a large white spot having some black behind it and many small white spots; each lateral extension dark on posterior side, reddish anteriorly (Figs. 46, 47). Venter of abdomen light gray. Female similar except having much red pigment on carapace and abdomen. Two horns between anterior median eyes. Lateral eyes on tubercles. Anterior median eyes much larger than posterior medians. Anterior medians two-thirds their diameter apart. Posterior medians one diameter apart, their radius from laterals. Total length of female 1.9 mm. Carapace 0.73 mm long, 0.68 mm wide. First femur, 1.69 mm; patella and tibia, 1.63 mm; metatarsus, 1.72 mm; tarsus, 0.60 mm. Second patella and tibia, 1.04 mm; third, 0.62 mm; fourth, 1.33 mm. Total length of male 1.5 mm. Carapace 0.60 mm long, 0.57 mm wide. First femur, 1.54 mm; patella and tibia, 1.62 mm; metatarsus, 1.60 mm; tarsus, 0.55 mm. Second patella and tibia, 0.91 mm; third, 0.60 mm; fourth, 1.17 mm.

Diagnosis. The male of this species is readily distinguished by the distal diagonal hook on the palpal conductor (Fig. 45). The epigynum depression has a median posterior septum (Fig. 44) and the connecting ducts are very short (Fig. 43), unlike other Central American species. The abdomen lacks dorsal nipples (Fig. 47).

Records. Costa Rica: San Isidro del General, 600-1200 m, ♂ (D. Rounds). *Panama Canal Zone:* Forest Reserve, 4-6 July, 1939, ♀ paratype (A. M. Chickering).

EPISINUS ASPUS sp. n.

Figures 48-51

Type. Male holotype from Musawas, Waspuc River, Nicaragua, 30 Sept. 1955 (B. Malkin), in the American Museum of Natural History. The specific name is an arbitrary combination of letters.

Description. Carapace yellow-white, dusky on sides. Eye region reddish. Sternum gray. Legs yellow-white. Abdomen reddish and black around border of dorsum; center of dorsum with white pigment in male, without pigment in female; venter reddish in female, dusky in male. Anterior median eyes seemingly larger than others, about one-third their diameter apart. Posterior median eyes less than one diameter apart, touching laterals. Pigment around base of lenses makes it difficult to see their exact shape. The females have horns between eyes, but these are absent in males. Abdomen subtriangular (Fig. 51), smooth, lacking nipples. Total length of female 2.2 mm. Carapace 0.71 mm long, 0.62 mm wide. First femur, 1.50 mm; patella and tibia, 1.42 mm; metatarsus, 1.36 mm; tarsus, 0.60 mm. Second patella and tibia, 0.85 mm; third, 0.58 mm; fourth, 1.17 mm. Total length of male 1.5 mm. Carapace 0.62 mm long, 0.55 mm wide. First femur, 1.48 mm; patella and tibia, 1.59 mm; metatarsus, 1.32 mm. Second patella and tibia, 0.85 mm; third, 0.65 mm; fourth, 1.17 mm.

Diagnosis. The distal margin of embolus base is almost at right angles to the long axis of the palpus (Fig. 50), while it is diagonal in the related *E. panamensis.* The median anterior dark spot of the epigynum (Fig. 49) and the longer seminal receptacles and shorter connecting ducts (Fig. 48) distinguish females from *E. panamensis.*

Record. One ♀ paratype collected with holotype.

EPISINUS BIMUCRONATUS (Simon), new combination

Figures 52-54

Sphyrotinus bimucronatus Simon, 1894, Histoire Naturelle des Araignées, 1: 551, *nomen nudum;* 1894, Ann. ent. Soc. France, 64: 144. Female holotype from San Esteban, [Aragua], Venezuela, in the Muséum National d'Histoire Naturelle, Paris, examined.

Description. Carapace yellow-white with silvery pigment between eyes and dark pigment behind anterior median eyes. Sternum, legs whitish-yellow. Abdomen with white pigment spots on dorsum and posterior (Fig. 54). No horns in eye region. Diameter of anterior median eyes equal to radius of other eyes. Lateral eyes on tubercles. Anterior median eyes one and one-half diameters apart, almost touching laterals. Posterior median eyes one-third diameter apart, one-quarter diameter from laterals. Abdomen wider than long with a median anterior hump and two posteriorly directed humps (Fig. 54). Some stronger setae on dorsum of distal end of patellae and some on tibiae. Total length 1.4 mm. Carapace 0.54 mm long, 0.44 mm wide. First femur, 1.04 mm; patella and tibia, 1.00 mm; metatarsus, 0.84 mm; tarsus, 0.40 mm. Second patella and tibia, 0.68 mm; third, 0.46 mm; fourth, 0.76 mm.

EPISINUS BICORNIGER (Simon), new combination

Figures 55-57

Theridium bicorne Keyserling, 1891, Die Spinnen Amerikas, Brasilianische Spinnen, 3: 193, pl. 7, fig. 140, ♀, ♂. Male and female syntypes from Serra Vermelha, [Est. Rio de Janeiro], Brazil, in the British Museum, examined. Not *T. bicorne* Wider.

Janulus bicornigera Simon, 1894, Histoire Naturelle des Araignées, 1: 517. New name for *T. bicorne* Keyserling.

Abdomen subtriangular as related species. Total length of female 2.2 mm. Total length of male 1.7 mm.

EPISINUS JUAREZI Levi

Episinus juarezi Levi, 1955, Jour. New York Ent. Soc., 62: 74, figs. 5, 6, 30, 31, 42, 43, ♀, ♂. Male holotype from Tamaulipas, Mexico, in the American Museum of Natural History.

Distribution. Tamaulipas, San Luis Potosí to Oaxaca, Mexico.

EPISINUS CHIAPENSIS Levi

Episinus chiapensis Levi, 1955, Jour. New York Ent. Soc., 62: 76, fig. 7, ♂. Male holotype from Las Ruinas de Palenque, Chiapas, Mexico, in the American Museum of Natural History.

Distribution. Known only from Chiapas, Mexico.

EPISINUS NADLERI Levi

Episinus nadleri Levi, 1955, Jour. New York Ent. Soc., 62: 77, figs. 12, 28, 29, 37, ♀, ♂. Female holotype from South Bimini, Bahama Islands, in the American Museum of Natural History.

Distribution. Bahama Islands and Jamaica.

Additional Record. Jamaica: The Great Morass, 25 March 1955, ♂ (A. M. Nadler, AMNH).

EPISINUS NEBULOSUS (Simon), new combination

Figures 64-68

Janulus nebulosus Simon, 1895, Ann. Soc. ent. France, 64: 135. Female holotype from Serra de Communaty, Prov. Pernambuco, Brazil, in the Muséum National d'Histoire Naturelle, Paris, examined.

Janulus germaini Simon, 1895, *ibid.*, 64: 136. Female holotype from Paraguay in the Muséum National d'Histoire Naturelle, Paris, examined. NEW SYNONYMY.

Note. Female holotype of *J. nebulosus* has a label indicating that it comes from Sa. Communaty, an unknown location placed by Simon at times in the neighboring state of Ceara.

Description. Carapace with sides brownish, darker than middle. Sternum, legs yellow-brown; ends of segments slightly darker. Abdomen with scattered fine black spots and some white pigment spots anteriorly on dorsum, between humps and around sides. Venter of abdomen gray, darker on sides than in middle. Two horns in eye region. Lateral and posterior eyes on tubercles. Abdomen about as wide as long (Fig. 67). Epigynum openings distinct (Fig. 66); two duct loops in ventral view if cleared and one loop visible in dorsal view of female genitalia (Figs. 64, 65). Total length 2.8 mm. Carapace 0.82 mm long, 0.74 mm wide. First femur, 1.40 mm; patella and tibia, 1.62 mm; metatarsus, 1.36 mm; tarsus, 0.36 mm. Second patella and tibia, 0.86 mm; third, 0.64 mm; fourth, 1.12 mm.

The holotype of *J. germaini* is a younger adult female still showing a dorsal abdominal pattern (Fig. 68). The epigynum and internal genitalia are like those of the holotype of *J. nebulosus*.

EPISINUS BICRUCIATUS (Simon), new combination

Figures 69-72

Janulus bicruciatus Simon, 1895, Ann. Soc. ent. France, 64: 136. Female holotype from Mato Grosso, Brazil, in the Muséum National d'Histoire Naturelle, Paris, examined.

Description. The whole specimen yellow-white except some pigment behind anterior median eyes and silvery around other eyes. Abdomen with indistinct longitudinal gray band having two cross bands (Fig. 72), a black mark on venter above pedicel, a distinct round black spot on posterior side of each lateral tubercle and a white pigment line on each side of spinnerets outside of which is a black mark. Horns between eyes large; lateral and posterior median eyes on tubercles. Abdomen subtriangular with tubercles more distinct from ventral view. Total length 2.6 mm. Carapace 0.76 mm long, 0.68 mm wide. First femur, 1.52 mm; patella and tibia, 1.60 mm; metatarsus, 1.50 mm; tarsus, 0.54 mm. Second patella and tibia, 0.84 mm; third, 0.62 mm; fourth, 1.14 mm.

EPISINUS SALOBRENSIS (Simon), new combination
Figures 73-78, Map

Janulus salobrensis Simon, 1895, Ann. Soc. ent. France, 64: 135. Two female syntypes from Salobro [near Vargito on old maps], Bahia, Brazil, in the Muséum National d'Histoire Naturelle, Paris, examined.

Episinus erythrophthalmus, — Levi, 1955, Jour. New York Ent. Soc., 62: 74, figs. 24, 25, 36. Not *E. erythrophthalmus* (Simon).

Description. The two type specimens are almost colorless yellowish, the only pigment being silvery behind eyes; sides of carapace slightly darker than middle. Posterior sides of abdomen slightly reddish, some small white pigment spots, and a larger white spot on each side of spinnerets. Horns between eyes small; lenses of lateral and posterior median eyes on tubercles. Abdomen subtriangular (Fig. 77). Total length of one female syntype 2.0 mm. Carapace 0.80 mm long, 0.70 mm wide. Legs broken off.

Figures 73-75 and 77 were prepared from a syntype.

The female has been described previously (Levi, 1955). The anterior lateral margins of the oval depression of the epigynum are more or less sclerotized. Although the specimen previously described had red eyes, no others seen have red pigment in the eye region. Only fragments of males collected with females were available.

Records. Lesser Antilles. Trinidad: Simla near Arima, 12 Dec. 1954, ♀; 28 Dec. 1954, ♀ (A. M. Nadler, AMNH); Port of Spain, 1913, ♀ (R. Thaxter). *British Guiana:* Kuyuwini Landing, Kuyuwini River, 20 Nov. 1937, ♀, ♂ fragments (W. G. Hassler, AMNH). *Brazil. Pernambuco:* Recife (SMF).

EPISINUS ZURLUS sp. n.

Figures 58-63

Type. Male holotype from Venezuela (E. Simon) in the Muséum National d'Histoire Naturelle, Paris (no. 13529). The name is an arbitrary combination of letters.

Note. Although it is poor practice to describe new species without accurate locality data, I have done so here because a number of specimens, both male and female, are available. Also, it is known that Simon, who collected the specimens, travelled in only a small region of Venezuela: from the Caracas vicinity to Tovar, Aragua, to Valencia, Puerto Cabello and San Esteban, Carabobo. The specimens were in the Paris collections, mixed up with specimens of *E. erythrophthalmus* and labelled as such.

Description. Carapace yellow-white, some pigment behind anterior median eyes, silvery between other eyes, sternum, legs yellow-white. Abdomen posteriorly and sides gray, center of dorsum with white pigment spots and some gray pigment; venter light gray, darker toward sides. Carapace with relatively small horns between eyes (Fig. 62). Anterior median eyes much larger than lenses of other eyes, which are on tubercles. Abdomen without dorsal nipples (Fig. 62). Total length of females 2.5 mm. Carapace 0.68 mm long, 0.64 mm wide. First femur, 1.56 mm; patella and tibia, 1.44 mm; metatarsus, 0.86 mm; tarsus, 0.42 mm. Second patella and tibia, 0.84 mm; third, 0.60 mm; fourth, 1.04 mm. Total length of male 1.6 mm. Carapace 0.62 mm long, 0.56 mm wide. First femur, 1.52 mm; patella and tibia, 1.56 mm; metatarsus, 1.36 mm; tarsus, 0.56 mm. Second patella and tibia, 0.84 mm; third, 0.62 mm; fourth, 1.08 mm.

Diagnosis. The connecting ducts lead posteriorly from the openings (Figs. 58-61) unlike the similar *E. erythrophthalmus*. The transverse line between the openings is sometimes more anterior, sometimes more posterior, in different specimens (Figs. 60, 61). The males are distinguished from *E. erythrophthalmus* by the basal flare of the conductor, which projects ventrally, is sclerotized, and has small teeth on the margin (Fig. 63).

Records. Male and female paratypes collected with holotype.

EPISINUS ERYTHROPHTHALMUS (Simon)

Figures 79-93, Map

Janulus erythrophthalmus Simon, 1894, Proc. Zool. Soc. London, p. 525. Male and female syntypes from St. Vincent Island, Lesser Antilles, in the British Museum, examined. Not *E. erythrophthalmus*, — Levi, 1955.

Description. Specimens from Panama. Carapace yellowish with dusky border and dusky patches on each side. Sternum white. Legs yellowish with dusky marks. Dorsum of abdomen black behind and on sides; light central area with white spots (Figs. 86, 89). Venter with epigastric area gray and black patches on sides that are extensions of the lateral and posterior dorsal black areas. Female generally lighter and less distinctly marked than male; white spots more numerous and smaller, but also usually having the four dark marks on venter. Two horns between eyes. Anterior median eyes much larger than others. Posterior and lateral eyes on tubercles. Total length of female 2.00 mm. Carapace 0.62 mm long, 0.62 mm wide. First femur, 1.32 mm; patella and tibia, 1.44 mm; metatarsus, 1.28 mm; tarsus, 0.44 mm. Second patella and tibia, 0.78 mm; third, 0.54 mm; fourth, 0.98 mm. Total length of male 1.5 mm. Carapace 0.59 mm long, 0.55 mm wide. First femur, 1.32 mm; patella and tibia, 1.47 mm; metatarsus, 1.28 mm; tarsus, 0.47 mm. Second patella and tibia, 1.02 mm; third, 0.52 mm; fourth 1.04 mm.

Figures 80, 81, 90 were prepared from the syntypes.

Note. This species, apparently widespread and relatively common, is quite variable. At first it was thought that the specimens coming from Panama belong to three species; but, on careful comparison, they were all found to have the same proportions and only superficial differences in the epigynum and palpus. The seminal receptacles and more sclerotized parts of the palpus are similar. The differences seem to be due to different degrees of transparency of the epigynum and the position of the anterior transverse sclerotized piece (Figs. 81, 83, 85). The transparent palpal sclerites seem to be in slightly different positions in each individual (Figs. 90-93).

Distribution. Panama to Bolivia.

Records. Panama. Arraiján (A. M. Chickering); 8 km S of El Valle (A. M. Chickering). *Panama Canal Zone.* Forest Reserve; Madden Dam; Chilibre; Summit; Balboa; 3 km N of Paraiso (all A. M. Chickering). *Lesser Antilles. Tobago Isl.* (P. H. Johnson, BMNH). *Trinidad:* Simla near Arima (A. M. Nadler, AMNH). Piarco (A. M. Nadler, AMNH). *Venezuela.* ♀, ♂ (E. Simon, MNHN). *Dist. Fed.:* Caracas, 1887-1888, ♂ (E. Simon, MNHN). *Aragua:* Maracay (A. M. Nadler, AMNH). *British Guiana.* Kuyuwini Landing, Kuyuwini River (W. G. Hassler, AMNH). *Bolivia. Cochabamba:* El Palmar, Chaparé, 900-1000 m, Sept. 1956, ♂ (L. Peña, ISNB).

Index

Valid names are printed in italics. Page numbers refer to main references.

agreste, 10
albostriatus, 12
americanus, 5
amoenus, 14
aspus, 19
bicorne, 20
bicorniger, 20
bicruciatus, 21
bigibbosus, 9
bimucronatus, 20
bituberculatum, 8
brasilianus, 5
bruneoviridis, 11
chiapensis, 20
clementina, 13
cognatus, 13
colima, 17
dominicus, 15
dusenii, 10
emanus, 11
erythrophthalmus, 22
erythrophthalmus, 23
germaini, 21
gratiosus, 13
immundus, 8
implexus, 15
juarezi, 20
longipes, 13
malachinus, 14
moyobamba, 16
nadleri, 21
nebulosus, 21
panamensis, 18
pyrus, 17
recifensis, 8
salobrensis, 22
simplifrons, 13
teresopolis, 15
truncatus, 5
typicus, 10
unitus, 16
vaticus, 18
zurlus, 23

Figs. 1-4. *Episinus gratiosus* Bryant. 1. Female genitalia, dorsal view. 2. Epigynum. 3. Female. 4. Left male palpus.

Figs 5-7. *E. albostriatus* (Simon). 5. Female genitalia, dorsal view. 6. Epigynum. 7. Female.

Fig. 8. *E. recifensis* sp. n., palpus.

Figs. 9-11. *E. emanus* sp. n. 9. Female genitalia, dorsal view. 10. Epigynum. 11. Female.

Figs. 12-15. *E. typicus* (Nicolet). 12. Female genitalia, dorsal view. 13. Epigynum. 14. Female. 15. Palpus.

Figs. 16-22. *E. immundus* (Keyserling). 16, 21. Female genitalia, dorsal view. 17, 22. Epigynum. 18, 20. Female. 19. Sternum. 16-19. (Syntype from Belém, Brazil). 20-22. (Huánuco, Peru).

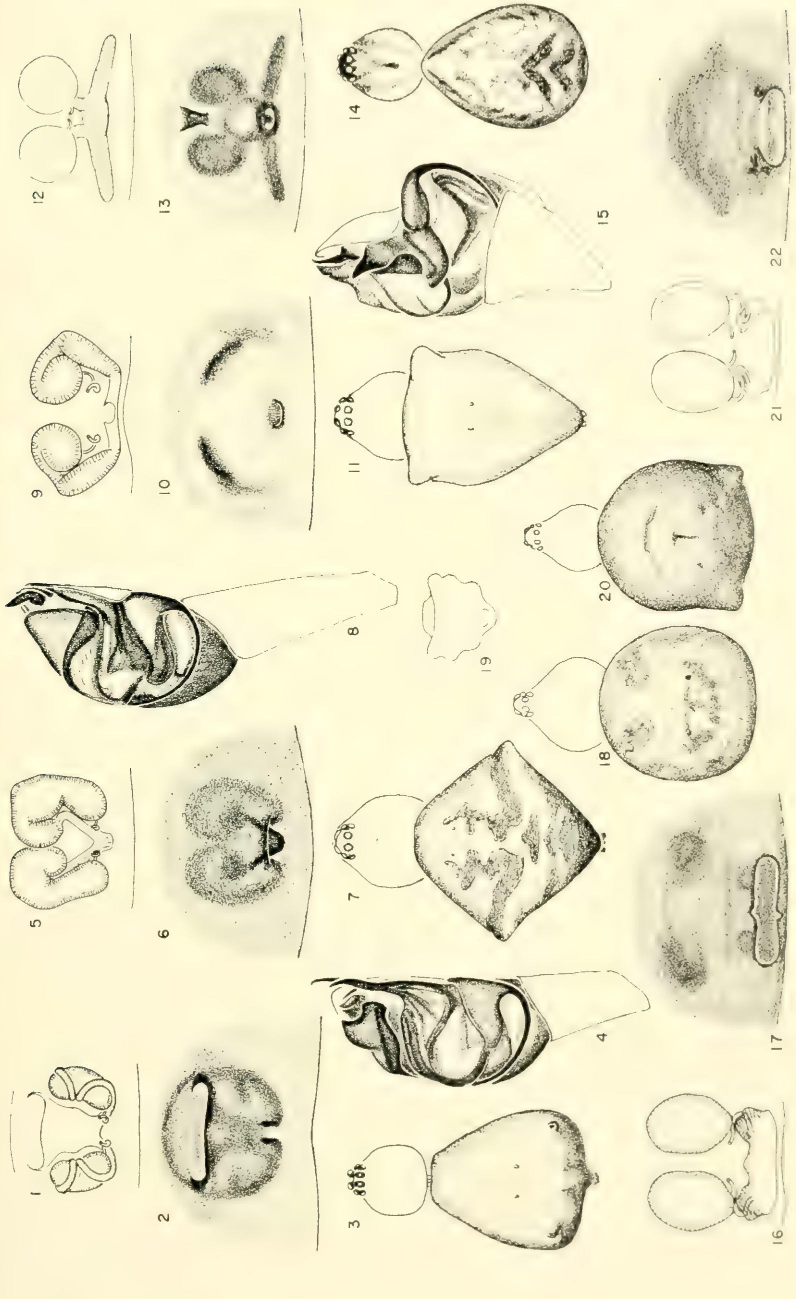


Fig. 23. *Episinus implexus* (Simon), juvenile abdomen, lateral view.

Figs. 24-26. *E. teresopolis* sp. n. 24. Female abdomen, lateral view. 25. Female genitalia, dorsal view. 26. Epigynum.

Figs. 27-29. *E. unitus* sp. n. 27. Female abdomen, dorsal view. 28. Female genitalia, dorsal view. 29. Epigynum.

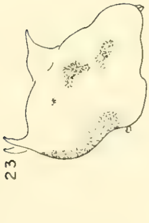
Figs. 30-33. *E. malachinus* (Simon). 30. Female abdomen, lateral view. 31. Female. 32. Female genitalia, dorsal view. 33. Epigynum.

Figs. 34-36. *E. pyrus* sp. n. 34. Female. 35. Female genitalia, dorsal view. 36. Epigynum.

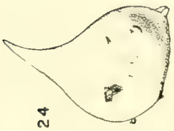
Figs. 37-39. *E. panamensis* Levi. 37. Female. 38. Female genitalia, dorsal view. 39. Epigynum.

Figs. 40-42. *E. moyobamba* sp. n. 40. Female abdomen, dorsal view. 41. Female genitalia, dorsal view. 42. Epigynum.

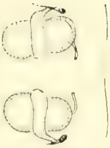
23



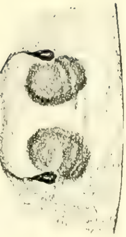
24



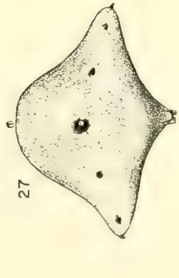
25



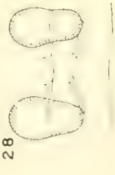
26



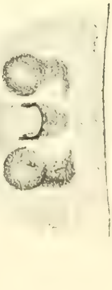
27



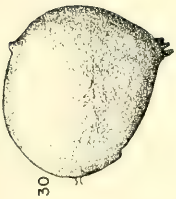
28



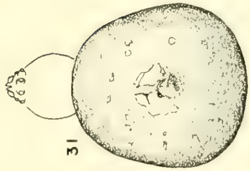
29



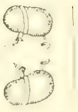
30



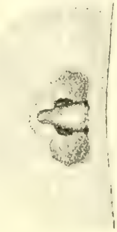
31



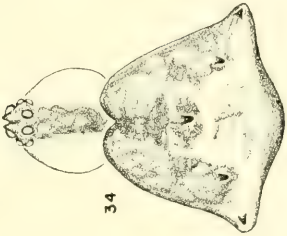
32



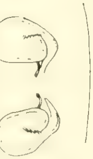
33



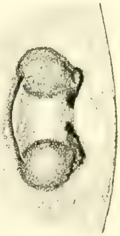
34



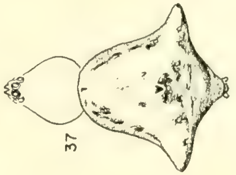
35



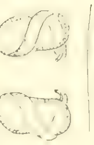
36



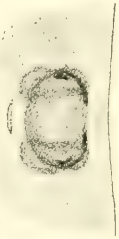
37



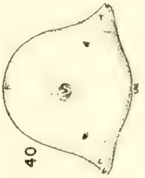
38



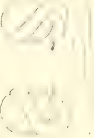
39



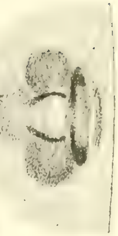
40



41



42



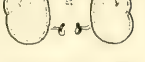
Figs. 43-47. *Episinus raticus* sp. n. 43. Female genitalia, dorsal view. 44. Epigynum. 45. Left male palpus. 46. Female. 47. Male abdomen.

Figs. 48-51. *E. aspus* sp. n. 48. Female genitalia, dorsal view. 49. Epigynum. 50. Palpus. 51. Female abdomen.

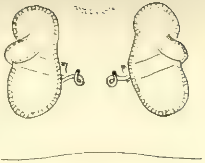
Figs. 52-54. *E. bimucronatus* (Simon). 52. Female genitalia, dorsal view. 53. Epigynum. 54. Female.

Figs. 55-57. *E. bicorniger* (Simon). 55. Epigynum cleared. 56. Epigynum. 57. Palpus.

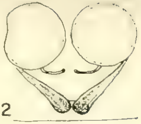
43



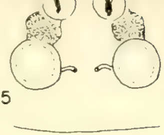
48



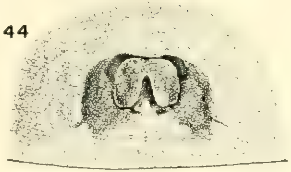
52



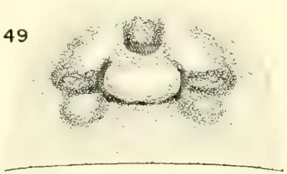
55



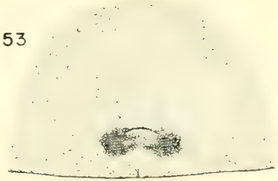
44



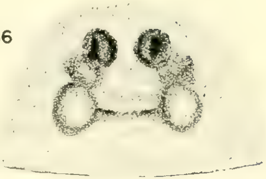
49



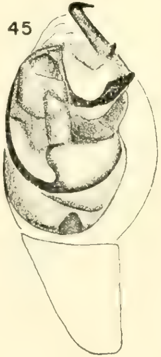
53



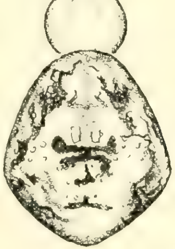
56



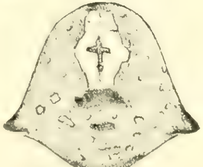
45



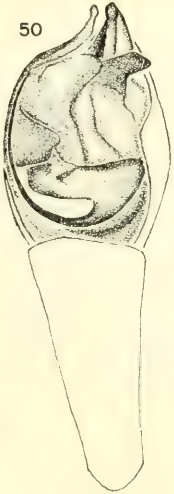
46



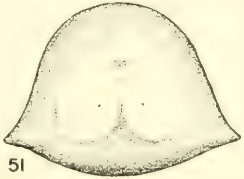
47



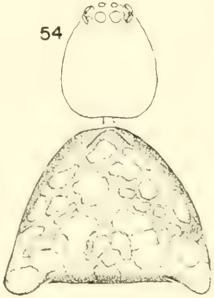
50



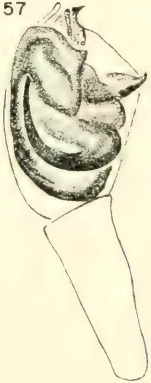
51



54



57

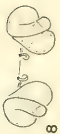


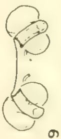
Figs. 58-63. *Episinus zurlus* sp. n. 58. Female genitalia, dorsal view. 59. Epigynum cleared. 60, 61. Epigynum. 62. Female. 63. Left male palpus.

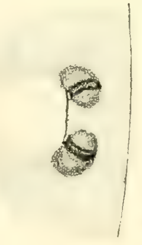
Figs. 64-68. *E. nebulosus* (Simon). 64. Female genitalia, dorsal view. 65. Epigynum cleared. 66. Epigynum. 67. Female. 68. Female abdomen. 64-67. Holotype. 68. Holotype of *Janulus germaini* Simon.

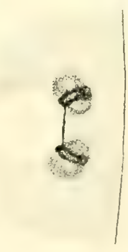
Figs. 69-72. *E. bicruciatus* (Simon). 69. Female genitalia, dorsal view. 70. Epigynum, cleared. 71. Epigynum. 72. Female.

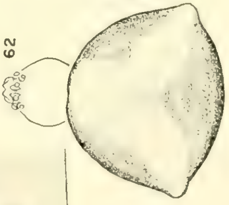
Figs. 73-78. *E. salobrensis* (Simon). 73. Female genitalia, dorsal view. 74. Epigynum, cleared. 75, 76. Epigynum. 77. Female. 78. Palpus. 73-75, 77. Syntype. 76. (Trinidad). 78. (Br. Guiana).

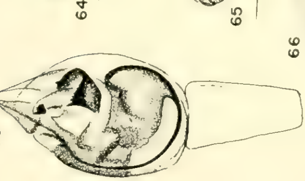

58

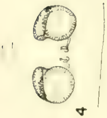

59

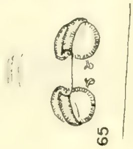

60

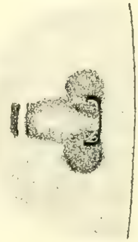

61

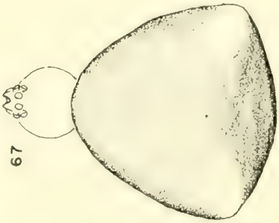

62

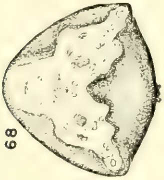

63

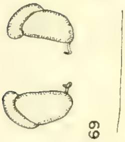

64

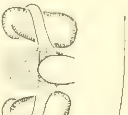

65

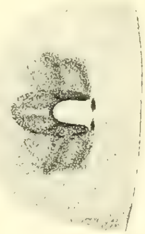

66

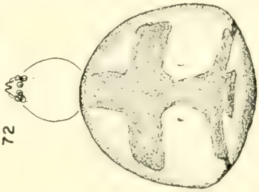

67

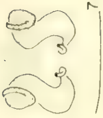

68

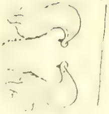

69

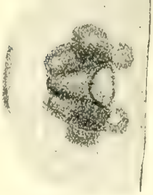

70

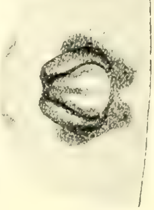

71

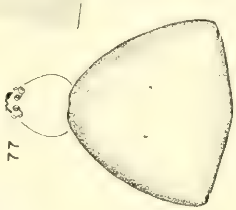

72

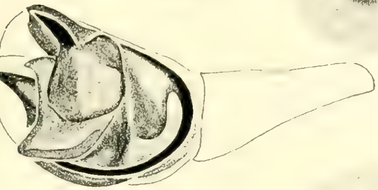

73


74

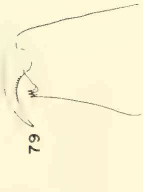

75

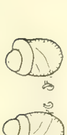

76

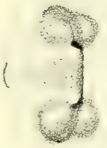

77

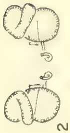

78

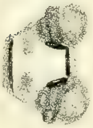
Figs. 79-93. *Episinus erythrophthalmus* (Simon). 79. Left chelicera of male, posterior view. 80, 82, 84. Female genitalia, dorsal view. 81, 83, 85. Epigynum. 86. Male. 87-89. Female. 90-93. Left male palpus. 79, 93. (Bolivia). 80, 81, 90. (Syntypes). 82-86, 88-89, 91-92. (Panama). 87. (Trinidad).

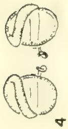

79

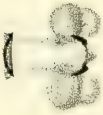

80

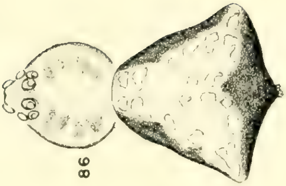

81

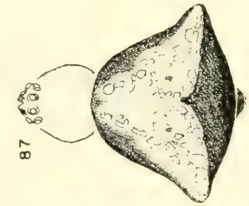

82

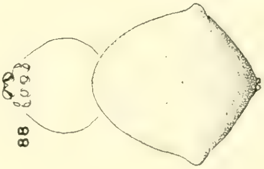

83

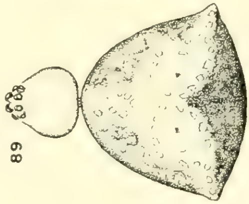

84

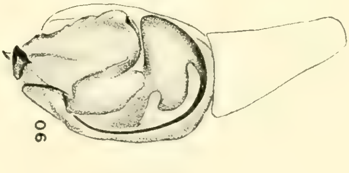

85

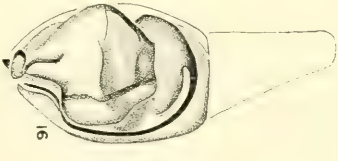

86

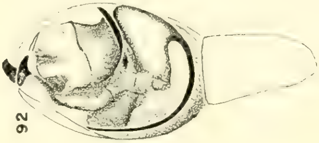

87

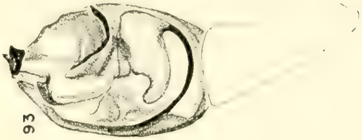

88


89


90


91


92


93

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 2

FOSSIL MAMMALS FROM THE LOWER PLIOCENE OF FISH LAKE VALLEY, NEVADA

By

John B. Clark, Mary R. Dawson and Albert E. Wood

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
March 30, 1964

PUBLICATIONS ISSUED BY OR IN CONNECTION WITH THE MUSEUM OF COMPARATIVE ZOOLOGY AT HARVARD COLLEGE

BULLETIN (octavo) 1863 — The current volume is Vol. 131.

BREVIORA (octavo) 1952 — No. 199 is current.

MEMOIRS (quarto) 1864–1938 — Publication was terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 41 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 28 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained from the Publications Office of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Of the Peters "Check List of Birds of the World," volumes 1, 4 and 6 are out of print; volumes 3, 5, 7, 9, and 15 are sold by the Museum, and future volumes will be published under Museum auspices.

The Proceedings of the First International Symposium on Natural Mammalian Hibernation edited by C. P. Lyman and A. R. Dawe is available as volume 124 of the Museum of Comparative Zoology Bulletin. Published in 1960, it consists of 26 papers and a general discussion, totalling 550 pages. Price $3.00 paper back, $4.50 cloth bound.

PUBLICATIONS OF THE BOSTON SOCIETY OF NATURAL HISTORY

The remaining stock of the scientific periodicals of the Boston Society of Natural History has been transferred to the Museum of Comparative Zoology for distribution. Prices for individual numbers may be had upon request.

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 2

FOSSIL MAMMALS FROM THE LOWER PLIOCENE OF FISH LAKE VALLEY, NEVADA

By

John B. Clark, Mary R. Dawson and Albert E. Wood

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
March, 1964

Bull. Mus. Comp. Zool., Harvard Univ., **131** (2): 27-63, March, 1964

No. 2 — *Fossil Mammals from the Lower Pliocene of Fish Lake Valley, Nevada*

By John B. Clark,[1] Mary R. Dawson[2] and Albert E. Wood[3]

INTRODUCTION

The material on which this study is based was collected by Wood, in 1935, from Hall's locality A (1930e, pl. 37, fig. 1) in the early Pliocene Fish Lake Valley beds, Esmeralda Formation, seven miles north of Arlemont, Nevada.

The material formed the basis for the unpublished Master's thesis, submitted to Amherst College, by Clark. In subsequent years it has proven impossible for him to complete the paper for publication, and the material has now been reworked by Dawson and Wood. Wood has brought up to date and revised Clark's manuscript for the rodents, and Dawson has done the same for the other forms.

The authors are grateful to Drs. J. T. Gregory, Donald Savage and R. A. Stirton for the loan of specimens; to Mrs. Katherine M. Reed and Drs. Claude Hibbard and Peter Robinson for discussions; and to Mrs. Frances W. Wood for critical reading and other assistance in preparation of the manuscript. Figures 6 and 7, B, C and D were drawn by Dr. Florence D. Wood. The material was collected while Wood was Cutting Traveling Fellow in Columbia University. The study has been assisted by the Dorothy Bridgman Atkinson Fellowship of the American Association of University Women awarded to Dawson, and by grants from the National Science Foundation and the Marsh Fund of the National Academy of Sciences to Wood. Abbreviations used are: M.C.Z., Museum of Comparative Zoology; S.D.S.M., South Dakota School of Mines and Technology; U. Cal., University of California Museum of Paleontology. We are grateful to the Museum of Comparative Zoology for undertaking the publication of this paper.

---

[1] Biology Department, Marietta College, Marietta, Ohio.

[2] Carnegie Museum, Pittsburgh, Pennsylvania.

[3] Biology Department, Amherst College, Amherst, Massachusetts.

Order INSECTIVORA

Family TALPIDAE

DOMNINOIDES cf. RIPARENSIS Green, 1956

Figure 1

Material: M.C.Z. Nos. 17887, incomplete left lower jaw having M_1, M_2-M_3 (broken), alveoli of P_4; 17888, incomplete left lower jaw having M_2, alveoli of P_4, M_1, M_3; 17889, left M_2 (broken).

In size (Table 1) and in most general characteristics these specimens resemble the type and only previously reported specimen of *Domninoides riparensis,* S.D.S.M. No. 53170, from the Clarendonian Wolf Creek faunule of South Dakota (Green, 1956, pp. 152-154). Compared to teeth in the type specimen, M.C.Z. No. 17889 is less worn, M.C.Z. No. 17887 is slightly more worn, and M.C.Z. No. 17888 is much more worn.

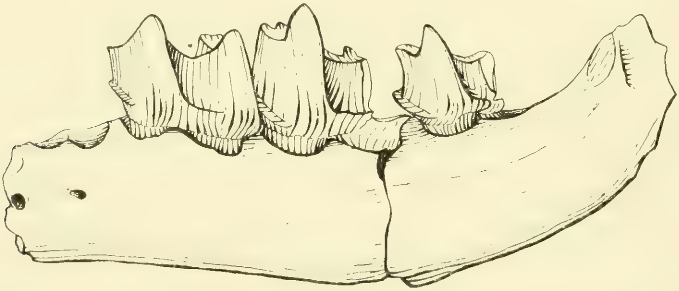


FIG. 1. *Domninoides* cf. *riparensis.* Lateral view of left lower jaw, M.C.Z. No. 17887, × 9.

The most distinct difference from the type specimen is exhibited by M.C.Z. No. 17887 (Fig. 1), which has on M_1 a small but distinct anterior cingulum that connects to the anterolingual cuspule. The anterior wall of M_1 in the type is smoothly convex, lacking a cingulum. Another difference appears on M_3 in M.C.Z. No. 17887, which has an anterior cingulum that is more reduced buccally than in S.D.S.M. No. 53170. Also, in the type specimen the metastylid of M_1 is larger than that of M_2, whereas in M.C.Z. No. 17887 the metastylid of M_2 is prominent and a distinct metastylid is absent on M_1.

The taxonomic significance of these differences is questionable in light of the few available specimens. Possibly the variation in the anterior wall of M_1 is a matter of individual diversity. Somewhat similar individual variation has been reported in another fossil talpid, *Mesoscalops scopelotemos*, in which there is "variable development of a small anterior cingulum, which appears in the majority of specimens" (Reed, 1960, p. 4). That the size of the anterior cingulum may vary with wear in the Fish Lake Valley talpid is shown by the fact that the cingulum on the well worn M_2 of M.C.Z. No. 17888 is narrower than that of M.C.Z. No. 17887. Similarly, stage of wear could account for the difference between the type and M.C.Z. No. 17887 in the cingulum of M_3.

Since wear and individual variation are perhaps responsible for the differences between the Fish Lake Valley talpid and the type of *D. riparensis*, a definite specific assignment should wait until more specimens allow better estimation of the range of variation in either population.

Variation that can be recognized as individual is exhibited by the two jaws from Fish Lake Valley, which differ from one another in the position of the two mental foramina. In both jaws, as in the type, the anterior foramen is below P_3. One specimen, M.C.Z.No. 17888, resembles the type in having the more posterior foramen in line with the posterior wall of the alveolus of P_4, whereas M.C.Z. No. 17887 has the posterior foramen farther forward, in line with the middle of P_4.

TABLE 1

Measurements (in millimeters) of *Domninoides* cf. *riparensis*

	M.C.Z. No. 17887	M.C.Z. No. 17888
M_1 length	*ca.* 2.3	—
width trigonid	1.4	—
width talonid	1.7	—
M_2 length	—	2.4
width trigonid	1.7	1.7
width talonid	—	1.6
alveolar length M_1-M_3	*ca.* 6.5	6.1
outside depth jaw, at middle of M_1	2.2	2.1

Order ?INSECTIVORA

Figure 2

A toothless fragment of a left lower jaw, M.C.Z. No. 17900 (Fig. 2), represents an unidentifiable species of small mammal. The alveoli of the penultimate tooth, with the anterior wall broken away, and of the last tooth indicate that the penultimate tooth was somewhat larger than the last. The alveolus of the last tooth is 1.4 mm long. The alveolus for the root of the trigonid of the last tooth is set obliquely to the long axis of the jaw, directed anterolingually to posterobuccally, and is longer on the lingual side. The alveolus for the root of the corresponding talonid is longer anteroposteriorly and narrower transversely than that of the trigonid. The wall between the two alveoli of the last tooth has an indistinct, shallow groove dorsally, and that between the two alveoli of the penultimate tooth is more distinctly grooved. The deep masseteric fossa is bounded anteriorly by a rounded ridge. Lingually the surface of the jaw is essentially smooth; a dental foramen occurs near the posterior edge of the incomplete specimen. Below the last tooth, the jaw is 1.5 mm deep.

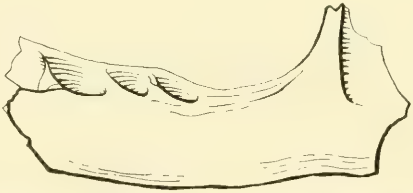


FIG. 2. ?Insectivore. Lateral view of left lower jaw fragment, M.C.Z. No. 17900, × 8.

Compared to other known members of the Fish Lake Valley fauna, M.C.Z. No. 17900 shows closest resemblance to *Mystipterus vespertilio*, the type and only reported specimen of which is a broken fragment of a jaw with M_3 (U. Cal. No. 29604). In both there is a deep masseteric fossa, and lingually both jaw fragments are essentially smooth. The toothless jaw is a little larger than the type of *Mystipterus vespertilio* and seems to have the anterior border of the ascending ramus relatively farther from the last tooth. The specimens are too incomplete to allow more than partial comparisons, and M.C.Z. No. 17900 is regarded as indeterminate.

In the course of these comparisons the question arose again of the taxonomic assignment of *Mystipterus*, originally described as a vespertilionid bat and compared with *Miniopterus* by Hall (1930a, p. 319). Re-examination of the characters of *Mystipterus* and of the differences from *Miniopterus* led Patterson and McGrew (1937, pp. 256-257) to assign the former to the insectivore family Soricidae. The features of *Mystipterus* cited by Patterson and McGrew as characteristic of soricids occur in some other insectivores as well. The deep masseteric fossa, for example, is found also in *Nyctitherium*, *Micropternodus* (Matthew, 1909, pl. 51, fig. 1), and a geolabidine insectivore, cf. *Myolestes dasypelix* (McKenna, 1960, p. 147). The combination of characters known in *Mystipterus* may not preclude reference to the Soricidae, but at the same time they do not seem to make such a reference the only assignment possible. It would seem necessary to have specimens of *Mystipterus* in addition to the rather inadequate type in order to clarify the taxonomic position of the genus.

Order LAGOMORPHA

Family OCHOTONIDAE

HESPEROLAGOMYS[4] new genus

Type species: Hesperolagomys galbreathi n. sp.

Diagnosis: Cheek teeth hypsodont but rooted; occlusal surface of P^4-M^1 with persistent crescentic valley, hypostria extending almost to crescent, and anteroloph transversely wider than posteroloph; P_3 with buccal fold between trigonid and talonid, anterointernal groove in trigonid, lingual wall short anteroposteriorly; trigonid of P_4-M_2 wider and shorter than talonid, talonid with anterior protrusion directed toward trigonid, and posterolophid present in early stage of wear; large mental foramen below P_3, smaller mental foramina anterior to P_3 and in line between M_1-M_2; lower teeth include M_1-M_3; size near that of *Oreolagus nevadensis;* tooth measurements as given in Table 2.

HESPEROLAGOMYS GALBREATHI[5] n. sp.

Figures 3-4

Type: M.C.Z. No. 17890, incomplete right lower jaw with broken incisor, P_3-M_2, and alveolus of M_3.

---

[4] From Greek: *hesperos* — west; *lagos* — hare; *mys* — mouse.

[5] For Dr. E. C. Galbreath in recognition of his work on fossil lagomorphs.

Hypodigm: Type; M.C.Z. Nos. 17891, fragmentary left lower jaw with P_3-M_2; 17892, fragmentary left lower jaw with talonid of P_4 to M_2; 17893-17894, upper incisors; 17895-17899, isolated upper cheek teeth; 7651-7652, isolated lower cheek teeth. Probably referable, U. Cal. No. 29633, upper deciduous premolar.

Diagnosis: As for the genus.

Description: The skull, with the exception of a maxillary fragment, is unknown, and the upper dentition is represented by isolated teeth only. The anterior upper incisor has a longitudinal groove slightly medial of center on its anterior surface. The part of the incisor medial to the groove protrudes farther anteriorly than does the lateral part. Of the upper cheek teeth, P^2 and P^3 are not known, but P^4 and probably M^1 are represented. Unilateral hypsodonty is exhibited by these teeth, which are convex lingually (Fig. 3 A, C, D). Two small buccal roots and a larger lingual root are present on the known upper cheek teeth.

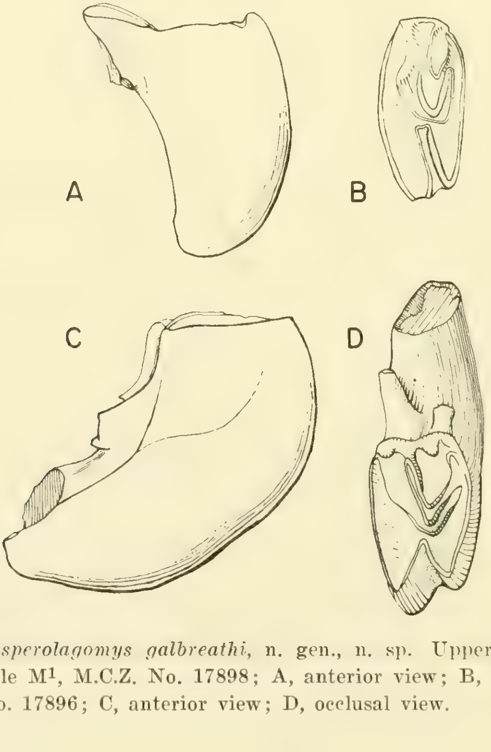


FIG. 3. *Hesperolagomys galbreathi*, n. gen., n. sp. Upper cheek teeth, × 9. Probable M^1, M.C.Z. No. 17898; A, anterior view; B, occlusal view. P^4, M.C.Z. No. 17896; C, anterior view; D, occlusal view.

On a worn P^4, M.C.Z. No. 17895, the anterior loph is wider than the posterior loph. The pattern on the occlusal surface includes an isolated, cement-filled, crescentic valley in the buccal half of the tooth and a cement-filled internal hypostria. The hypostria is directed toward the anterior wall of the crescent and extends almost to its lingual wall. Features of the buccal edge of the occlusal surface cannot be determined due to breakage. Another specimen, M.C.Z. No. 17896 (Fig. 3 C, D), seems to be a relatively unworn P^4. At the occlusal surface the anterior and posterior lophs are nearly equal in width, but farther down the shaft the anterior loph protrudes more medially. A central lobe connects to the buccal wall between two rounded cuspules and extends in a wide V to join the posterior wall of the tooth. Anterior, lingual, and posterolingual to the central lobe is the cement-filled depression that forms the crescentic valley of the more worn tooth. Posterobuccal to the lobe is a second cement-filled depression. The buccal exits of these depressions are blocked by the buccal cuspules. The internal hypostria crosses about one-third of the occlusal surface.

A worn tooth, M.C.Z. No. 17898 (Fig. 3 A, B), probably is a molar. In this specimen the anterior loph protrudes farther lingually than the posterior loph; the complete width of the anterior loph is not shown, owing to its broken lingual wall. The crescentic valley divides anterobuccally into two distinct parts around a transversely elongated cuspule. The anterobuccal part of the valley seems to be better developed than in M.C.Z. No. 17895, a P^4 in an approximately comparable stage of wear. The probable molar lacks the posterobuccal cuspule and is reduced posterobuccally in comparison with M.C.Z. No. 17896, although valid comparisons with the latter are limited by differences in stage of wear. Interpretation of M.C.Z. No. 17898 as a molar is supported by comparisons with *Amphilagus fontannesi*, a late Miocene ochotonid in which M^1 resembles this probable molar and P^4 is more similar to M.C.Z. No. 17896. The closer resemblance of M.C.Z. No. 17898 to M^1 than to M^2 of *A. fontannesi* suggests that it may be the anterior molar, since M^2 is more reduced posteriorly in *A. fontannesi* (Forsyth Major, 1899, pl. 36, figs. 6 of M^2, 7 of M^1, 8 of P^4).

An isolated upper tooth, U. Cal. No. 29633, was tentatively identified as *Entoptychus?* sp. (Hall, 1930c, p. 296) but was subsequently recognized as a deciduous premolar of a lagomorph (Wood, 1936c, p. 25). The tooth is smaller than the permanent upper teeth of *Hesperolagomys*, but probably represents this ochotonid rather than the much larger leporid of the Fish Lake Valley fauna.

The lower jaw and dentition are more adequately represented than the upper. The ventral border of the horizontal ramus (Fig. 4 B) is essentially straight below the cheek teeth and curves up, below the diastema. The jaw is slightly deeper below the posterior than below the anterior cheek teeth. The shape of the jaw is more similar to that in *Titanomys* and *Oreolagus* than to that in *Ochotona*, in which the jaw is deeper below the anterior cheek teeth and has a more concave dorsal border at the diastema.

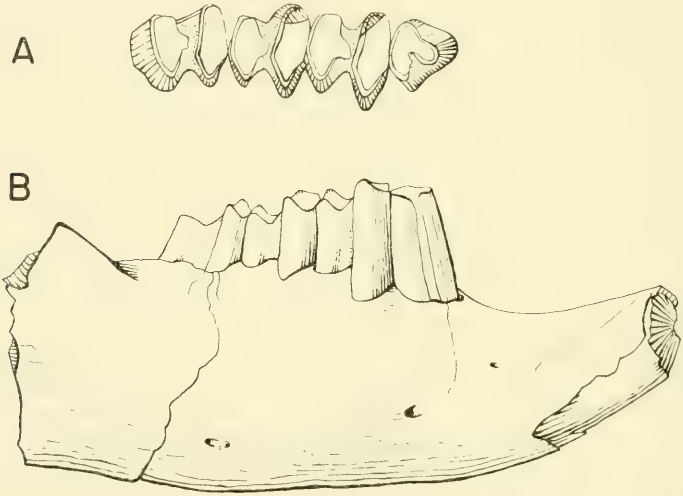


FIG. 4. *Hesperolagomys galbreathi*, n. gen., n. sp. Right lower jaw with P_3-M_2, type, M.C.Z. No. 17890, × 6. A, occlusal view of cheek teeth; B, lateral view.

On the lateral surface of the jaw are several mental foramina; the largest of these is in line with the talonid of P_3 and below mid-depth of the jaw. A smaller foramen occurs anterior to P_3, above mid-depth, and a depression with two small foramina is situated in a line between M_1 and M_2 and lower than the anterior foramina. This disposition of mental foramina, with the middle foramen the largest, differentiates *Hesperolagomys* from other known ochotonids. In *Desmatolagus vetustus*, *D. gobiensis*, and *Sinolagomys* (Bohlin, 1942, pp. 62-63), anterior and posterior mental foramina are present. Between them there occurs in some specimens another small foramen or foramina approximately in the position of the large foramen in *Hesperolagomys*. Presence of a series of mental foramina seems to be primitive for lagomorphs. Different ochotonids retain and emphasize different foramina of this series. *Hesperolagomys* retains a primitive series, with emphasis on the middle foramen. Another variant on these foramina in an ochotonid is seen in *Kenyalagomys* of the Miocene of Africa, in which the two main mental foramina (MacInnes, 1953, p. 10) seem to correspond to the middle and posterior foramina of *Hesperolagomys*. In *Ochotona* the single mental foramen, probably representing the posterior foramen of *Hesperolagomys*, is situated below M_2.

The shaft of the incisor extends approximately to a line below the middle of M_1, as indicated by a swelling on the medial surface of the jaw. The lower cheek teeth are hypsodont but rooted. For most of their length the trigonid and talonid of P_4-M_2 are connected by cement only, but a short distance above the roots the dentine of the two columns becomes confluent. An isolated tooth, probably a molar, shows two small rootlets for the trigonid and a single root for the talonid. The alveolar portions of P_3 and P_4 are relatively straight anteroposteriorly and extend down lateral to the shaft of the incisor. The lateral surface of the jaw swells out over P_4, thus giving space for that tooth lateral to the incisor. The alveolar portions of M_1 and M_2 curve posteriorly and in this way avoid interfering with the shaft of the incisor.

The most complete lower jaw is the type specimen, M.C.Z. No. 17890 (Fig. 4). On P_3 a cement-filled buccal fold crosses about half the occlusal surface and marks the division between trigonid and talonid. The trigonid is rounded anterobuccally. Anterolingually, P_3 has a wide, shallow groove with a thin coating of cement. This groove is interpreted here as being in the trigonid, and not between trigonid and talonid. The lingual wall of P_3 is short anteroposteriorly.

The trigonids of P_4-M_2 are wider transversely and shorter anteroposteriorly than the corresponding talonids. Each talonid sends forward a narrow protrusion. Enamel is prominent on the external and posterior walls of trigonids and talonids. The alveolus of M_3 is rounded buccally and is narrower transversely than that of the talonid of M_2. The shape of the alveolus suggests that M_3 was probably more rounded and less tapered buccally than is that tooth in *Ochotona*.

A young individual of *Hesperolagomys* is represented by U. Cal. No. 29626, an incomplete lower jaw with P_4-M_1 (Hall, 1930c, p. 311; the specimen was tentatively identified by Hall as *Sylvilagus*? sp.). Small posterolophids, which would be worn away a short distance down the tooth, occur on the talonids of the two teeth. The limited hypsodonty of *Hesperolagomys* is illustrated by this specimen, in which the little worn P_4 shows at its base the confluence of the dentine of the columns that occurs just above the roots.

TABLE 2

Measurements (in millimeters) of *Hesperolagomys galbreathi*

	M.C.Z. No. 17895 P^4	M.C.Z. No. 17896 P^4	M.C.Z. No. 17898 probably M^1
length	1.5	1.5	1.3
width anteroloph	—	2.3	2.9
width posteroloph	—	2.2	2.5

	M.C.Z. No. 17890 type specimen
P_3 length	1.1
width	1.2
P_4 length	1.7
width trigonid	1.9
width talonid	1.4
M_1 length	1.6
width trigonid	1.8
width talonid	1.4
M_2 length	1.6
width trigonid	1.7
width talonid	1.4
alveolar length P_3-M_3	8.1
length P_3-M_2	5.8
length P_4-M_2	4.9
inside depth jaw, at middle of M_1	5.3

Hesperolagomys is an ochotonid that retained into the early Pliocene a number of primitive characteristics, among which are the rooted cheek teeth, persistence of folds in the buccal part of the occlusal surface of P^4 and M^1, and talonids that are narrower transversely than the trigonids on P_4-M_2. Combined with these primitive characteristics, *Hesperolagomys* exhibits its own peculiar features, including the marked anterior protrusion of the talonids on P_4-M_2 and the disposition of the mental foramina.

Other ochotonids that have been reported from the North American later Tertiary are *Oreolagus* from the Miocene and *Ochotona* which first appears in the middle Pliocene. Among the characters distinguishing *Oreolagus* from *Hesperolagomys* are, in the former, higher crowned cheek teeth, shape and proportions of the lower cheek teeth, in which the trigonids and talonids of P_4-M_2 are more nearly equivalent in width, and absence of M_3. *Ochotona* is distinguished from *Hesperolagomys* by its more hypsodont cheek teeth, absence of a persistent crescentic valley on P^4 and M^1, more complex folds on P_3, and approximately equivalent width of the columns of P_4-M_2. The presence of *Hesperolagomys* with its primitive characteristics in the North American early Pliocene seems to be a parallel to the presence of *Amphilagus fontannesi*, an ochotonid likewise having primitive dental features, in the late Miocene of Europe.

Unless there has been a reversal of evolution affecting several characteristics, which seems unlikely, *Hesperolagomys* was derived from a primitive ochotonid. Of known forms, *Desmatolagus*, which has rooted cheek teeth and a generally primitive level of development, could be near the ancestry of *Hesperolagomys*. More specific evidence for such an affinity, other than the merely primitive features, is afforded by the structure of P_3. In *Hesperolagomys* that tooth has a narrow lingual exposure and an anterointernal groove that seems to be in the trigonid. *Desmatolagus gobiensis* of the late Oligocene of Asia has a somewhat similarly shaped P_3 in some individuals; in late stages of wear the anterointernal groove is worn away in that species. An earlier species, *D. vetustus* of the Mongolian early Oligocene, shows the same general pattern of folding on P_3, but the lingual wall is less reduced anteroposteriorly than in *D. gobiensis* (Burke, 1941, pp. 16-17) and *Hesperolagomys*. A trigonid of P_3, that is divided by an anterior fold, and an internal wall of P_3, that becomes reduced in later species, are among the characters distinctive of Burke's "*Desmatolagus* phylum" (1941, pp. 17, 22). If the folds on P_3 in *Hesperolagomys* have been interpreted correctly, the similar structure of that tooth would seem to indicate affinity with *Desmatolagus*. Whether *Hesperolagomys* is closer to Asian species of *Desmatolagus* or to North American species referred to that genus remains to be determined.

Family LEPORIDAE

HYPOLAGUS FONTINALIS Dawson, 1958

Material: M.C.Z. Nos. 7640, incomplete left lower jaw with P_4-M_2; 7641, left premaxilla with upper incisors; 7642, isolated teeth; 7643, postcranial fragments including proximal and distal ends of humerus, astragali, calcanea, navicular.

Hypolagus fontinalis, a previously known member of the Fish Lake Valley fauna (Dawson, 1958, p. 48), is represented by these specimens. Lower cheek teeth agree in size (Table 3) and structure with other specimens of this species.

The upper cheek teeth of *H. fontinalis* were previously unknown. Two folds, of which the lingual is longer, occur on the anterior surface of P^2. The internal hypostria crosses somewhat more than half the width of the occlusal surface on P^3-M^2. The walls of the hypostria are strongly crenulated on P^3; on specimens that are probably P^4 or M^1 the walls are less strongly crenulated; and in a specimen that seems to represent M^2 the walls are only slightly wavy. Thus, the folding in the walls of the hypostriae decreases posteriorly in the series of molariform teeth. In general structure the upper cheek teeth resemble those of *H. vetus*, a species averaging larger in size than *H. fontinalis*.

TABLE 3

Measurements (in millimeters) of *Hypolagus fontinalis*

	M.C.Z. No. 7642	M.C.Z. No. 7640	M.C.Z. No. 7643
P^2 length	1.2		
width	2.6		
P^4 or M^1 length	2.3		
width anteroloph	4.2		
width posteroloph	4.0		
P_3 length	2.6		
width trigonid	2.0		
width talonid	2.5		
P_4-M_2 length		7.4	
astragalus, length proximodistal			10.6
width			5.4
humerus, length proximal end			10.9

The postcranial parts are smaller than corresponding parts of *H. vetus* but suggest similarity to *H. vetus* in general level of development.

Order RODENTIA

Family CRICETIDAE

COPEMYS Wood 1936

Type species: Hesperomys loxodon Cope 1874.

Referred species: C. dentalis (Hall), *C. longidens* (Hall), *C. kelloggae* (Hoffmeister), and *C. esmeraldensis* n. sp.

Distribution: Late Miocene Barstow and Niobrara River to early Pliocene Fish Lake Valley; Nebraska, New Mexico, California and Nevada.

Emended diagnosis: Cricetid in which alternation of buccal and lingual cusps has begun to develop; crowns low; no distinct mesocone or mesoconid, although mesoloph or mesolophid may be well developed; protoconid and metaconid of M_1 unite, after varying amounts of wear, at anterior end of protoconid; metaconid of M_{2-3} at anterior margin of tooth, with anterior cingulum absent or restricted to buccal margin of tooth; paracone of M^1 unites with posterior end of protocone and, sometimes, with its anterior end; metacone of M^1 unites with posteroloph rather than with hypocone; metacone of M^2 tending to unite in this manner; lower incisors broad; mental foramen below or just in front of M_1; masseteric fossa prominent, ending below M_1; deep valley between M_3 and the coronoid process.

One of the striking peculiarities of North American Tertiary rodent history is the record of the cricetids. In the middle Oligocene, *Eumys* is unquestionably the most abundant rodent, and a number of different species have been recognized. *Leidymys* and *Scottimus* have developed from a *Eumys* ancestry. Species of *Eumys* are known from the Oligocene of the Great Plains (Wood, 1937; Galbreath, 1953) and of Montana (Wood, 1937, p. 262; White, 1954, pp. 410-415). In the early Miocene, two species of *Leidymys* and *Paciculus insolitus* are known from the middle John Day (Wood, 1936a). *Eumys eliensis*, from the equivalent Fort Logan of Montana (Black, 1961c, pp. 7-10), seems to be more closely related to *E. brachyodus* of the plains than to the large Montanan species of *Eumys* described by White (1954). It seems possible that *Cotimus* (Black, 1961a) may be related to *Paciculus,* known only from the upper teeth (Wood, 1936a, pp. 4-6; Black, 1961c, pp. 10-12). *Scottimus kellamorum* is a continuation of the Oligocene *Scottimus* lineage (Black, 1961b).

The only described North American cricetids between the early Miocene and the late Pliocene are: *Horatiomys montanus* (Wood, 1935b, if it is a cricetid), and *Paciculus montanus* (Black, 1961c) from the Deep River of Montana; *Cotimus alicae* from the Flint Creek of Montana (Black, 1961a); *Miochomys niobrariensis* from the Niobrara River (Hoffmeister, 1959); and four species of *Copemys* — *C. longidens* (Hall) from the late Miocene Barstow of California, *C. kelloggae* (Hoffmeister) from the late Miocene Niobrara River of Nebraska, *C. loxodon* (Cope) from the late Miocene or early Pliocene Santa Fé of New Mexico, and *C. dentalis* (Hall) from the early Pliocene Fish Lake Valley. Another species of *Copemys* from the Fish Lake Valley is described below.

The published record would indicate that the cricetids were nearly absent from the Great Plains area during the Miocene and most of the Pliocene, although they survived and evolved in the intermontane areas farther west. Even at such a semi-intermontane area as Split Rock there are no cricetids among the thousands of rodent teeth known. The dominant North American Miocene small rodents were the entoptychine geomyids. In the Pliocene, their place seems to have been taken by the heteromyids. The cricetids do not come back into the picture until the end of the Pliocene, when both hesperomyine and microtine forms become abundant. Perhaps the invasion of the Old World microtines reduced the competing heteromyids, and allowed the native American cricetids to spread eastward once more. The presence of *C. kelloggae* in Nebraska and of cricetids in the Miocene of Florida (Wood, 1947, p. 491), however, shows that they were not completely absent in the great plains and farther east.

The present evidence suggests that the hesperomyines were derived from the eumyines in a manner somewhat similar to that shown in Figure 5, and that the series *Eumys* — *Leidymys* — *Copemys* — *Peromyscus* is not far from a true phyletic sequence. The citation of *Leidymys* in the Oligocene is based on the reference to that genus of *L. vetus* (Wood, 1937, p. 257). Galbreath (1953, p. 72) states that in his opinion *Eumys exiguus* and *Leidymys vetus* represent the same species. In this allocation he is followed by Black (1961b, p. 3). However, *Leidymys* is characterized by a well-developed hypocone-like cusp on M^3. In *Eumys*, including *E. exiguus*, this cusp is at most an enlarged cingulum. Since *Leidymys* is presumably derived from *Eumys*, the transition must have occurred as individual variants. But *Eumys exiguus* also shows the development of anteroposterior connections between the crests, leading toward *Scottimus* (Black, 1961b, p. 3, transfers it to *Scottimus*, which is just as reasonable as leaving it in *Eumys*), and there is no trace of these in the type of *Leidymys vetus*. The status of the Oligocene eumyine rodents

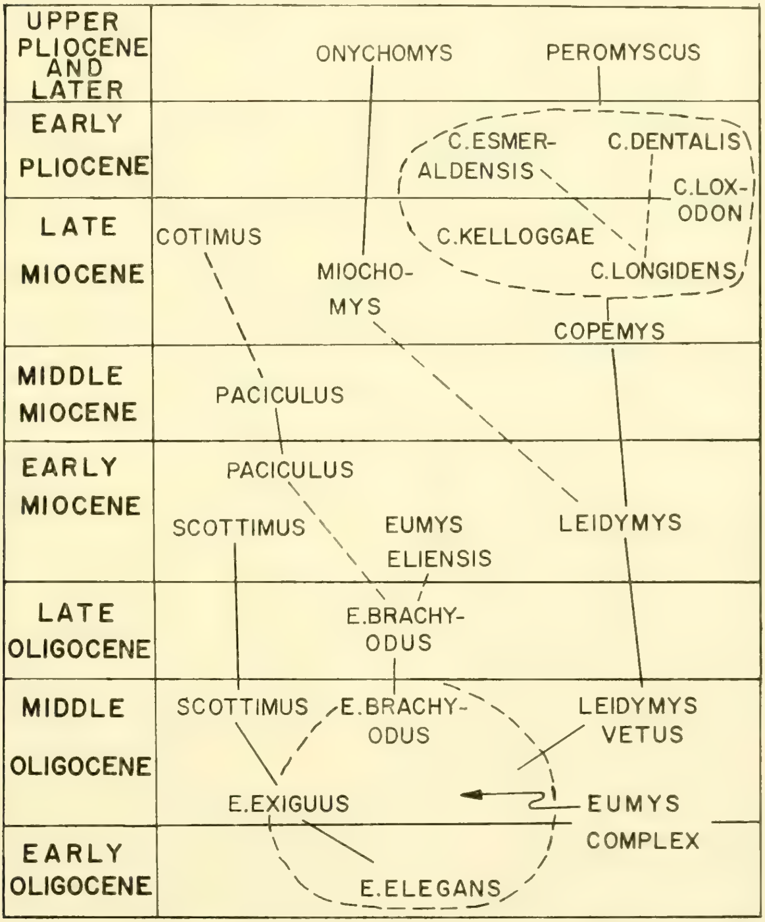

UPPER PLIOCENE AND LATER
EARLY PLIOCENE
LATE MIOCENE
MIDDLE MIOCENE
EARLY MIOCENE
LATE OLIGOCENE
MIDDLE OLIGOCENE
EARLY OLIGOCENE
ONYCHOMYS
PEROMYSCUS
C.ESMERALDENSIS
C.DENTALIS
C.LOXODON
C.KELLOGGAE
C.LONGIDENS
COTIMUS
MIOCHOMYS
COPEMYS
PACICULUS
PACICULUS
SCOTTIMUS
EUMYS ELIENSIS
LEIDYMYS
E.BRACHYODUS
SCOTTIMUS
E.BRACHYODUS
LEIDYMYS VETUS
E.EXIGUUS
EUMYS COMPLEX
E.ELEGANS

FIG. 5. Phylogenetic relationships of North American Tertiary cricetids.

will have to remain nebulous until the very extensive collections are studied, so that it will become possible to separate individual variations from specific and generic variants. There is so much variation among North American Oligocene cricetids that all possible later trends seem to be represented within a single population, sometimes even in the material from a single ant hill. Very few if any of the described forms can be considered to be adequately categorized and separated from each other.

Cotimus (Black, 1961a, p. 73) is distinct from *Copemys*. It may represent the hitherto undescribed lower teeth of *Paciculus*. At any rate, as stated above, it is close to that genus, and not in the line leading to *Peromyscus*.

Hoffmeister (1959, p. 698) has pointed out the similarities of *Miochomys* to *Onychomys* (Fig. 5). The former genus is most probably also derivable from *Leidymys*. *Horatiomys* is as isolated as when it was first described (Wood, 1935b, p. 3).

Copemys includes several forms at rather diverse levels of development. All the species seem to be evolving in slightly different directions, and the data are not adequate at present to determine ancestor-descendant relationships among the group. The alternation of the buccal and lingual cusps and the shifts in the points of attachment of the various cusps and crests are progressive features foreshadowing *Peromyscus*.

COPEMYS LOXODON (Cope)

Figures 6-7

Hesperomys loxodon Cope, 1874, p. 148.
Eumys loxodon (Cope). Cope, 1875, p. 993.
Peromyscus loxodon (Cope). Hay, 1902, p. 727.
Copemys loxodon (Cope). Wood, 1936a, p. 5.

The synonymy given here, rather than that cited previously by Wood (1936a, pp. 5-6), is the correct one.

Type: U.S.N.M. No. 1204, right lower jaw with I_1 and M_{1-2}; an isolated right I^1 may belong to the same form, and an isolated right I_1 certainly does not.

Hypodigm: Type only.

Emended diagnosis: Well developed lingual mesolophids, extending from posterior arm of protoconid to lingual margin of crown and ending in a distinct mesostylid; posterior cingulum of M_2 connecting with buccal rather than lingual margin of hypoconid; masseteric fossa with everted, overhanging dorsal margin; tooth measurements as given in Table 4.

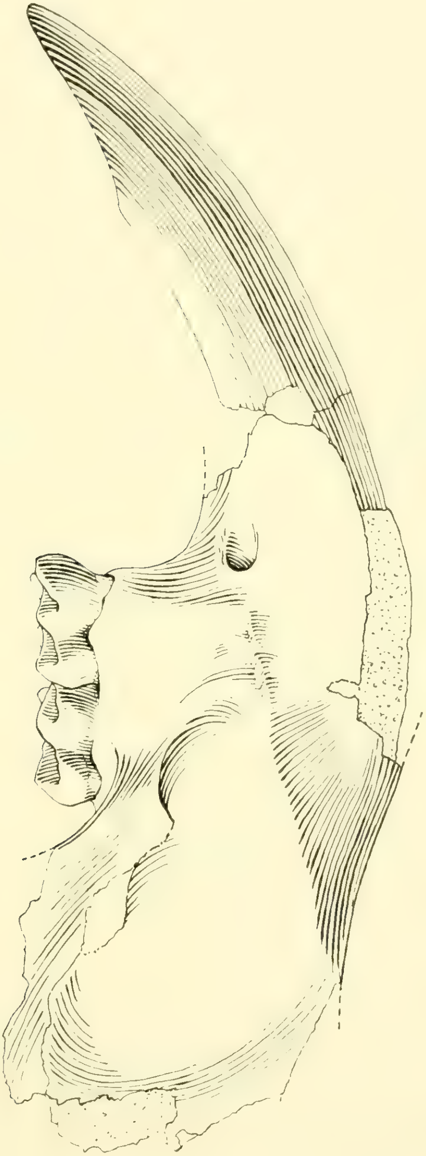


Fig. 6. *Copemys loxodon*, U.S.N.M. No. 1204, lateral view of lower jaw, × 10.

Description: The masseteric fossa is quite unusual, in its overhanging dorsal margin (Fig. 6). No suggestion of such a structure is seen in other species referred to this genus, but there is clearly considerable interspecific variability in this respect (Figs. 8E, 9F). The ventral margin of the fossa extends to the ventral border of the angular process, as in *C. dentalis.* The masseteric knob, at the front of the fossa, lies beneath the middle of M_1, and is more distinct than in *C. dentalis,* but less so than in *C. esmeraldensis.* The mental foramen lies just in front of the anterior root of M_1 as in the other species. There is a pronounced groove between M_3 and the coronoid process. The latter passes the alveolar border by the middle of M_3.

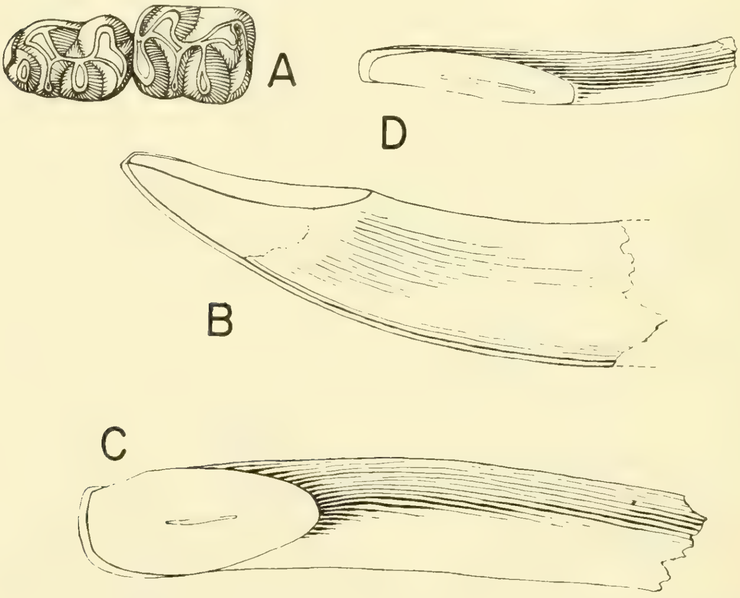


Fig. 7. *Copemys loxodon,* U.S.N.M. No. 1204, × 10. A, RM_{1-2}; B, medial view of right lower incisor; C, ventral view of right upper incisor; D, dorsal view of another right lower incisor with same number.

The cheek teeth of the only known specimen of this species are quite distinctive (Fig. 7A), and are farther removed from the *Peromyscus* pattern than are those of the other members of the genus. As suggested by Wood (1936a, p. 6), the closest relatives of this species seem to be "certain species from the Miocene and

Pliocene of California and Nevada, which have been described as *Peromyscus*," and which are here referred to *Copemys*. The peculiar position of the posterior cingulum of M_2 is just as unique as it seemed in 1936 (*op. cit.*, p. 6), but Hooper's recent study (1957) of tooth variation in *Peromyscus* shows how much variability can exist within a single living genus, and warns us to be careful about drawing the lines of specific or generic variation too tightly among fossil forms. (The magnification shown for these teeth in Wood, 1936a, fig. 5, is incorrect, that figure being 7.5, rather than 5, times natural size.)

The lower incisor (Figs. 6, 7B) is similar to that of other species of the genus. The anterior face is fairly flat. At the tip of the median side, there is an extensive flat area, where there has been interdental wear with the tooth of the opposite side. This is also present on the type of *C. dentalis,* but all other specimens are too broken to be sure whether this is a generic character, although it probably is. It would probably be associated with a well-developed Transversus mandibulae muscle.

The upper incisor associated with this specimen (Fig. 7C) is of the correct size and general shape to belong here, but it cannot with certainty be referred to this form. Another lower incisor (Fig. 7D) is much too small for *Copemys,* and is too narrow and with too heavy an anterior enamel face to belong to a cricetid. It agrees in size, shape, and shape of the pulp cavity with the incisor of small heteromyids, and presumably is referable to a member of that family.

COPEMYS DENTALIS (Hall)

Figure 8

Peromyscus dentalis Hall, 1930c, p. 306.

Type: U. Cal. No. 29635, a lower jaw with RI_1 and M_{1-2}.

Hypodigm: Type, and U. Cal. No. 29636, edentulous right jaw, and U. Cal. No. 29638, left jaw with M_{1-2}.

Emended diagnosis: Fossa between M_3 and the coronoid process bears small nutritive foramina; mental foramen below diastema as in *C. loxodon;* anteroconid area of M_1 simple as in *C. longidens,* but larger than in *C. loxodon;* mesolophid present or absent, and low when present; no distinct hypoconulid on M_1; metaconid of M_{2-3} far forward, eliminating lingual half of anterior cingulum as in *C. loxodon;* lower incisor narrow; tooth measurements as given in Table 4.

Description: The tooth pattern of this species (Fig. 8 A-B) is more *Peromyscus*-like than is that of the genotype. The teeth show the *Peromyscus* type of alternation of cusps, but the cusps are still less completely integrated with the lophs than in *Peromyscus*, warranting the reference of this species to a genus ancestral to *Peromyscus*, for which *Copemys* is the best name until a great deal more is known about Miocene and early Pliocene North American cricetids.

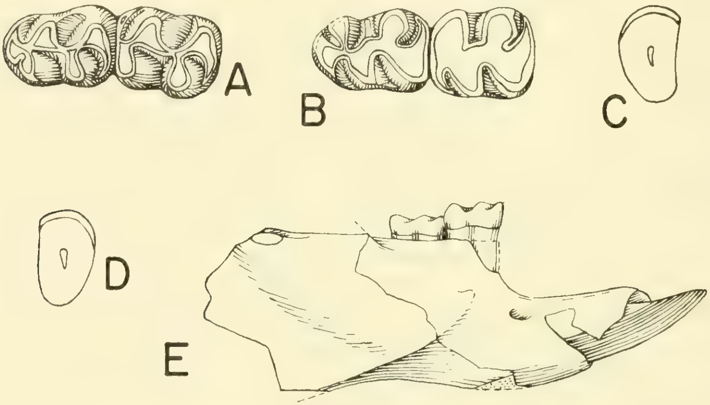


FIG. 8. *Copemys dentalis.* Teeth × 10, jaw × 5. A, U. Cal. No. 29635, RM$_{1\text{-}2}$, type; B, U. Cal. No. 29638, LM$_{1\text{-}2}$; C, U. Cal. No. 29635, type, cross section of right I_1, from rear; D, U. Cal. No. 29636, cross section of right I_1, from front; E, lateral view of lower jaw, anterior half based on U. Cal. No. 29635, type, and rear half on U. Cal. No. 29636.

In M$_1$, the anteroconid is somewhat larger than in *C. loxodon*, and is close to the metaconid. There are distinct ridges running posteriorly from the protoconid, along the buccal margin of the tooth, in all teeth. These are also present on M$_1$ of *C. loxodon* (Fig. 7 A), but are less well developed in other species. The mesolophid (or posterior arm of the protoconid) is absent in all teeth except M$_1$ of U. Cal. No. 29638, where it extends as a faint, low ridge to the buccal margin of the tooth (Fig. 8 B). The hypoconulid seems poorly developed on M$_1$, but distinct on M$_2$.

The incisor has a rounded anterior face with a heavy coat of enamel. It is slightly concave on the medial side of the type (Fig. 8 C) which is not shown in the other specimen (Fig. 8 D), and is probably due to crushing, and, at this level, is certainly not due to interdental wear.

The jaw is slender, with no suggestion of a chin process. The mental foramen is below the posterior portion of the diastema. The masseteric fossa is shallower than in other species of the genus, being bounded by faint ridges, especially on the dorsal side (Fig. 8 E). The anterior end of the fossa is beneath the middle of M_1. Posteriorly, the ventral border of the fossa approaches the ventral margin of the angle. The base of the incisor, in U. Cal. No. 29636, forms a knob on the lateral surface of the mandible, at the level of the molar alveoli but well behind them. This knob is broken through on the specimen.

COPEMYS LONGIDENS (Hall)

Peromyscus longidens Hall, 1930b, p. 315.
Peromyscus sp. Hall, 1930b, p. 316.
Peromyscus sp. Hall, 1930b, p. 316.

All of Hall's specimens seem to be within the limits of one variable species, in which variation is no greater than in living species of *Peromyscus* (Hooper, 1957).

There is a single anteroconid on M_1 of the type, as in the previously discussed species. A crest, probably the mesolophid, reaches the lingual margin of the crown in the type. It is much smaller in U. Cal. No. 28503. In U. Cal. No. 28506, the crest is complete but its lingual half is very low. The isolated tooth of Hall's first *Peromyscus* sp. (U. Cal. No. 28517; it is M_1, *not* P_4 as Hall stated) is about ten per cent smaller than the type specimen, and is somewhat (but not significantly) narrower than the other material. The isolated M_2 of U. Cal. No. 28516 is intermediate in size between what would be expected for that of U. Cal. No. 28517 and the rest of the population.

There is a faint trace of an anterolingual cingulum on M_2 of the type, but it is almost eliminated. The mesolophid is very short on this tooth.

The lingual anterior cingulum of M_3 is very small. In the type, the entoconid and mesolophid are minute. There is a lingual marginal ridge connecting the metaconid and entoconid.

The upper teeth show progressive development of lophs. In M^1 of U. Cal. No. 28515 the metaconid unites with the middle of the posterior cingulum. In M^2, there is the beginning of this posterior union (not shown in Hall's figure, 1930b, fig. 7 A), but the union between the metacone and hypocone is still present. The mesoloph (or anterior arm of the hypocone) is well developed. The tooth figured by Hall as M^3 (*op. cit.*, fig. 6) is actually a specimen of M^2 in which both unions of the metacone are present, and the mesoloph is very long.

The range of variation in tooth size is indicated in Table 4.

The mental foramen lies beneath the diastema, as in *C. dentalis*, and the size and shape of the masseteric fossa is also like that of *C. dentalis.*

COPEMYS KELLOGGAE (Hoffmeister)

Peromyscus kelloggae Hoffmeister, 1959, p. 698.

This species, from the late Miocene Niobrara River fauna of Nebraska is referable to *Copemys.* The anteroloph is a single cusp, close to the metaconid (Hoffmeister, 1959, fig. 1 B). There is a long mesolophid, reaching nearly to the lingual margin of the crown. The hypoconulid is very well developed.

The upper molar described by Hoffmeister as *Miochomys niobrariensis* does not appear to be referable to the same form as do the lower teeth, although they are of the appropriate size to belong together. The metacone has not shifted its union away from the hypocone, and the posterior cingulum is short. The separation of the tooth into three transverse lobes is not characteristic of *Copemys.*

COPEMYS ESMERALDENSIS n. sp.

Figure 9

Type: M.C.Z. No. 7644, right jaw with M_1 and M_3 and incisor.

Hypodigm: Type; M.C.Z. No. 7645, right jaw fragment with M_1; M.C.Z. No. 7646, edentulous right jaw; and M.C.Z. No. 7647, left maxillary fragment with M^1.

Diagnosis: Jaw heavier than in *C. dentalis.* with chin process; masseteric fossa not reaching as far ventrad on angle as in *C. dentalis* and upper border of masseteric fossa more pronounced, but much less so than in *C. loxodon;* mental foramen beneath M_1 rather than in front of it; fossa between M_3 and coronoid as in *C. dentalis;* anteroconid area highly complex; mesolophid present and long, though sometimes low; sometimes an accessory crest running buccad from the entoconid to the buccal margin of the tooth; hypoconulid of M_1 distinct; metacone of M^3 uniting with posterior cingulum rather than with hypocone; lower incisor wide; larger than *C. dentalis;* tooth measurements as given in Table 4.

TABLE 4

Measurements (in millimeters) of lower teeth of *Copemys*

	C. loxodon	*C. dentalis*			*C. esmeraldensis*			*C. longidens*		*C. kelloggae*		
	U.S.N.M. No. 1204	U. Cal. No. 29635	U. Cal. No. 29636	U. Cal. No. 29638	M.C.Z. No. 7644	M.C.Z. No. 7645	M.C.Z. No. 7646	U. Cal. No. 28502	O.R. of other specimens (after Hall, 1930a, p. 317)	U. Cal. No. 28517	U. Cal. No. 36105, Type (after Hoffmeister, 1959, p. 698)	U. Cal. No. 36158
	R	Type R	R	L	Type R	R	R	Type R		R	L	L
M_{1-3} alveolar			4.40	4.35	4.85		4.94	4.79	4.54-4.9			
M_1 anteroposterior	1.70	1.50		1.56	1.80	2.13		1.76	1.70-1.90	1.55	1.50	
width, metalophid	1.10	0.94		0.98	1.21	1.19		1.13		0.90	1.06	
width, hypolophid	1.15	1.08		1.08		1.31		1.21	1.13-1.23	1.03	1.16	
M_2 anteroposterior	1.57	1.40		1.37				1.57	1.50-1.70			
width, metalophid	1.22	1.09		1.15				1.28				
width, hypolophid	1.27	1.11		1.20				1.18	1.20-1.30			
M_3 anteroposterior					1.51			1.52	1.32-1.50			
width, metalophid								1.04	1.03-1.10			
width, hypolophid					1.00			0.93				
I_1 anteroposterior		1.27	1.26		1.40		1.44					
transverse		0.76	0.76		1.03		1.02					0.59

Distribution: Lower Pliocene Fish Lake Valley beds, Esmeralda Formation of Nevada. All material came from locality A shown by Hall (1930c, pl. 37, fig. 1).

Description: As shown by the two specimens of M_1 preserved in the present collection (Fig. 9 B, C) there is considerable variability in pattern in this tooth. From what is known of the variability in the Oligocene *Eumys*, and from the detailed studies of *Peromyscus* by Hooper (1957), however, it seems obvious that a great deal of individual variation can be expected within a single species of cricetid. Initially, because the specimens come from a single locality, all the Fish Lake Valley cricetids were referred to a single species. As the study proceeded, however, it became apparent that not only is the material in the present collection all much larger than Hall's material, but there is also the much greater complexity of the anteroconid region and the rather striking difference in the jaw structure, including the masseteric fossa and the position of the mental foramen. These differences make it seem unlikely that this material is conspecific with *C. dentalis*, even though the present collection came from the same spot as the University of California material.

The pattern of M^1 (Fig. 9 A) is fundamentally intermediate between that of *Eumys elegans* (Wood, 1937, fig. 57) and that of such living species of *Peromyscus* as *P. nudipes* (Hooper, 1957, fig. 19). The anterocone is a large cusp, continued both buccally and lingually by narrow ridges. Buccally, there are two such ridges, separated by a groove, as in *P. nudipes*. The anterior arm of the protocone unites with the middle of the anterocone. The posterior arm of the protocone unites with the paracone to form a protoloph as in *Eumys*. In general, in *Peromyscus*, the paracone is behind the protocone, though this is not always the situation. This shift is just beginning in the present form. The mure is longer than in *Peromyscus*. The mesoloph, as in *Eumys*, is a continuation of the anterior arm of the hypocone, instead of appearing more closely related to the paracone, as in *Peromyscus* (Hooper, 1957, figs. 9, 15, 16 and 19). The mesoloph is directed into the base of the metacone, rather than extending freely to or toward the buccal margin of the tooth as in *Paciculus* (Black, 1961c, fig. 4) or some species of *Peromyscus* (Hooper, 1957, figs. 18-19). The most progressive character of this tooth is the union of the metacone with the posteroloph, rather than with the hypocone. In this it resembles *C. dentalis* and is more advanced than *Miochomys niobrariensis*.

Even though this union is characteristic of *Peromyscus*, not all members of that genus are as advanced as is *Copemys dentalis*. The measurements of this specimen are: anteroposterior, 2.27 mm; width protoloph, 1.48; width metaloph, 1.52.

The two specimens of M_1 are rather different, as well as being in very distinct stages of wear. The unworn tooth (Fig. 9 C) shows that the anterolophid is a very complex area, being formed of an anteroconid (partly divided in two), a large lingual cusp, a buccal marginal crest from the anteroconid, and a long, narrow crest from the lingual cusp almost to the buccal margin. The worn specimen (M.C.Z. No. 7644, Fig. 9 B) cannot be shown to have had a different pattern. This area is much more complex than anything seen in any other species of *Copemys*, or in *Eumys*, though the beginnings of subdivision of the anteroconid may be seen in *E. obliquidens* (Wood, 1937, fig. 62) and *E. spokanensis* (White, 1954, fig. 47). This area is much more complicated than is the corresponding area of any of the *Peromyscus* teeth figured by Hooper, though it is approached in *P. nudipes* (Hooper, 1957, fig. 19). The protoconid and metaconid unite at the anterior end of the metaconid, the latter cusp being the more anterior. This condition is typical of both *Copemys* and *Peromyscus*, and is a contrast to *Eumys*, where the primary union is at the posterior side of the protoconid. In *C. loxodon*, the metaconid is more isolated than in *C. esmeraldensis*. The ectolophid (in the sense of Wood and Wilson, 1936; this ridge is called the mure by Hooper, 1957, fig. 1) is much longer than in *Eumys*, being like that of *Peromyscus* in this respect. What may be a mesolophid extends from the middle of the ectolophid almost to the lingual margin of the crown, not being as elevated as is the ectolophid (Fig. 9 C). In M.C.Z. No. 7644 (Fig. 9 B), the mesolophid looks as if it were perhaps more correctly identified as the posterior arm of the protoconid, as in some specimens of *Eumys* (Wood, 1937, fig. 58). There is a connection in this same specimen between this lingual crest and the anterior side of the entoconid (Fig. 9 B). The entoconid connects with the ectolophid in front of the hypoconid, rather than with the anterior arm of the hypoconid as in Oligocene species of *Eumys*, resembling *Eumys eliensis* (Black, 1961c, fig. 3 A) and *Peromyscus* in this respect. There is much more of a hypoconulid than in *Eumys*. An unusual crest that extends buccally from the point where the entoconid meets the ectolophid in one specimen (Fig. 9 C), is completely absent in the other (Fig. 9 B). This crest is present in many of the species of *Peromyscus* discussed by Hooper, the closest similarity being seen in *P. nuttalli* (Hooper, 1957, fig. 18). This crest, which seems to be fairly important in *Peromyscus*, has been called the ectolophid by Hooper. It is completely unrelated to the ectolophid as that term was used by Wood and Wilson (1936) and does not seem to have been discussed by anyone else. This crest is clearly a neomorph in *Copemys* and *Peromyscus*, and does not arise as a buccal extension of the mesoconid, which Wood and Wilson would have considered to be a buccal part of the mesolophid. Both of these teeth belong to Hooper's pattern type *g* (1957, p. 11). Of the species he studied, pattern *g* occurs in less than ten per cent of all except *P. maniculatus* (20%), *P. truei* (20%), *P. hylocetes* (25%), *P. oaxacensis* (60%) and *P. mexicanus* (50%). A well developed buccal crest (Hooper's ectolophid) is present in all *P. hylocetes* and *P. oaxacensis;* 90 per cent of *P. yucatanensis;* 80 per cent of *P. nasutus* and *P. difficilis;* 70 per cent of *P. boylei;* 30 per cent of *P. leucopus* and *P. mexicanus;* 20 per cent of *P. melanotis* and less than ten per cent of the remainder.

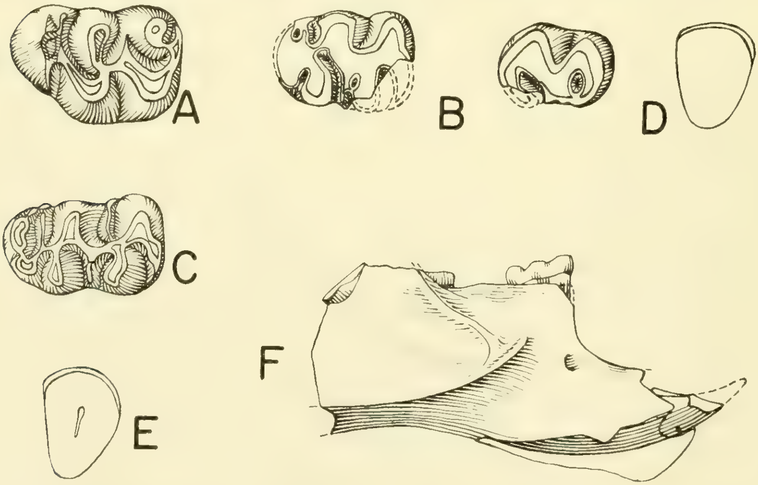


FIG. 9. *Copemys esmeraldensis* n. sp. Teeth × 10, jaw × 5. A, LM^1, M.C.Z. No. 7647; B, type, RM$_1$ and M$_3$, spaced as in the specimen, M.C.Z. No. 7644; C, RM$_1$, M.C.Z. No. 7645; D, cross section of RI$_1$, M.C.Z. No. 7644, type; E, cross section of RI$_1$, M.C.Z. No. 7646; F, lateral view of lower jaw, M.C.Z. No. 7644, type. Outline portion restored from M.C.Z. No. 7646. The incisor slid back into the alveolus before fossilization.

Therefore, as far as the available data go, *C. esmeraldensis* seems closest to *P. oaxacensis*, among the species studied by Hooper, in these respects.

The single specimen of M_3 (M.C.Z. No. 7644, Fig. 9 B) is both badly worn and broken. Hooper does not discuss this tooth in *Peromyscus*. This tooth is very different from that of *Eumys*. There is no anterior cingulum, and the metaconid is continuous along the anterior edge of the tooth to the protoconid. From here, a broad ridge runs to the lingual margin of the tooth, showing slight irregularities at the tooth margin, which suggests that it may include a mesolophid and an entoconid, the latter being well forward of the hypoconid. A broad posterolophid extends across the rear of the tooth.

The incisor is broad, with a rounded anterior face, and is proportionately wider and rounder, laterally, than in *C. dentalis*. The enamel is fairly thick, and extends well onto the lateral side of the tooth (Fig. 9 D-E). The pulp cavity enlarges toward the enamel-covered side of the tooth (Fig. 9 E). The base of the incisor is in the ascending ramus behind and at or above the level of M_3 (Fig. 9 F).

Three lower jaws are preserved permitting the composite restoration shown in Figure 9 F. There is a prominent chin process in M.C.Z. No. 7646, not preserved on the other specimens. Such a process does not seem to have been present in *C. dentalis* (Hall, 1930c, fig. 16). This difference may be sexual, but the overall differences in size and in tooth pattern suggest that it is not. The symphysis is weakly ridged, indicating that there may have been a strong Transversus mandibulae muscle and free movement between the mandibles. The alveolar border drops abruptly in front of M_1, as in *C. loxodon*, in contrast to its more gentle slope in *C. dentalis* and *C. longidens*. The prominent mental foramen lies beneath the anterior root of M_1, as in *C. loxodon*, instead of beneath the diastema as in the other species, and opens anterad rather than slightly upward. The masseteric fossa is broad and flat. The masseteric knob is clearly differentiated, beneath the posterior end of M_1, farther to the rear than in *C. dentalis* (Hall, 1930c, figs. 16-17). The masseteric fossa does not extend as far ventrally in the angle as in *C. dentalis*. The coronoid process passes the alveolar border by the middle of M_3. There is a prominent fossa between M_3 and the base of the coronoid, which contains one or more nutritive foramina, as in other species of the genus.

At the present time, little can be said of the interrelationships of the five species of *Copemys*. *C. esmeraldensis* is probably the closest to *Peromyscus*. *C. loxodon* is apparently the most aberrant. *C. longidens* may be ancestral to *C. esmeraldensis*. The differences between *C. longidens* and *C. dentalis* are not great except in size, which may not be very significant, phylogenetically. *Copemys kelloggae* is fairly close to *C. longidens* and *C. dentalis*. These three species are all closer to each other than any is to *C. esmeraldensis* or *C. loxodon*.

Family CASTORIDAE

EUCASTOR DIVIDERUS Stirton, 1935

Figure 10

Aside from lagomorph material, fragmentary remains of this beaver are the most abundant fossils in the collection. The present material adds some features to the full account of this species given by Stirton (1935, pp. 431-437). Two upper premolars, M.C.Z. Nos. 7648 and 7649, show interesting pattern variants, and M.C.Z. No. 7650 is an upper deciduous premolar, hitherto not described.

In both of the permanent premolars, the anteroloph is very long, covering the entire front of the tooth, as opposed to the earliest stage of wear figured by Stirton (1935, fig. 107). The parastria is present in one specimen (Fig. 10 A), but is converted to a parafossette in the other (Fig. 10 B). In each specimen, there is a small enamel lake, of very uncertain homology, in the middle of the paracone. The mesoflexus in the less worn specimen extends across the tooth to the posterior margin of the crown, where it forms a distinct flexus behind the hypocone (Fig. 10 A). In the more worn specimen, this is cut off from the posterior margin of the crown, as in Stirton's specimens. There is considerable variation in the region of the metaflexus. In Stirton's least worn tooth (1935, fig. 107), the metaflexus opens to the rear, and there is a small isolated lake behind it. In M.C.Z. No. 7648, the metaflexus is a triangular valley, opening posteriorly (Fig. 10 A). In the more worn premolar, the metafossette is widely separated from the rear of the tooth, resembling Stirton's second stage of wear (*op. cit.*, fig. 107), but retaining a minute lake behind the fossette.

Presumably these variants indicate that there are numerous minor irregularities at the surface of the unworn crown, and that these are highly variable, giving a variety of slightly different patterns with wear. The exact angle at which the wear surface cuts the crown may also make appreciable pattern differences.

The upper milk tooth (Fig. 10 C) is clearly deciduous, as it is much lower crowned than are the permanent teeth. There was a large single root under the anterior part of the crown, and two smaller ones under the posterior part. The anterior root, however, is proportionately smaller than in P^4. The hypostria and mesostria extend almost to the base of the crown. The metastria is long, but not quite as long as the other two. The mesoflexus and metaflexus interconnect, isolating a circular buccal mesostyle. The metaflexus runs transversely across the posterior part of the tooth, and is much more extensive than in P^4. The paraflexus is already transformed into a parafossette.

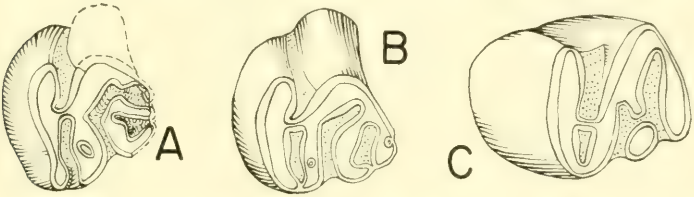


FIG. 10. *Eucastor dividerus*, × 5. A, RP^4, M.C.Z. No. 7648; B, RP^4, M.C.Z. No. 7649; C, RdP^4, M.C.Z. No. 7650.

Family HETEROMYIDAE

DIPRIONOMYS cf. PARVUS Kellogg, 1910

Two isolated and unassociated unworn cheek teeth are perhaps referable to this species: M.C.Z. No. 8535, RP^4, and M.C.Z. No. 8536, RM_2. Since the previously known material is badly worn, they add considerably to our knowledge of this rodent.

The premolar (Fig. 11 A) is clearly that of a heteromyine, in view of the two-cusped protoloph. The buccal cusp is quite small, and distinctly subsidiary to the main cusp. The metaloph forms a crest of nearly uniform height, running from the metacone to the hypostyle, and passing behind the slightly higher hypocone. The hypostyle is at about a right angle with the rest of the metaloph. The valley between the hypostyle and the hypocone curves buccad behind the latter, but would not persist very long with wear.

The molar (Fig. 11 B) is considerd to be M_2 rather than M_1 because of its anteroposterior diameter, which is less than would be expected in M_1 (cf. Wood, 1935a, Table II). Both lophs are strong, and the cusps form only minor enlargements. The protoconid is the only really distinct cusp. There is a prominent valley between the protoconid and protostylid, which would result in the formation of a Y-pattern, a characteristic heteromyine feature (Wood, 1935a, p. 165). The hypolophid is almost a straight crest, the cusps being very indistinct. The least depth of the central valley is between the two stylids, and the valley would thus become closed, buccally, after a moderate amount of wear. Slight further wear would unite the lophs just linguad of the bases of the protoconid and the hypoconid, isolating the buccal part of the valley as a lake. This double union is characteristic of *Diprionomys* (Wood, 1936b, p. 118).

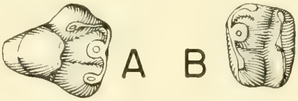


FIG. 11. *Diprionomys* cf. *parvus*, × 10. A, RP^4, M.C.Z. No. 8535; B, RM_2, M.C.Z. No. 8536.

These specimens are the first from the Fish Lake Valley beds that can be referred to *Diprionomys*, Hall's two species (*D. tertius* and *D. quartus*) being perognathines which Wood (1935a, pp. 92-96) placed in a separate genus, *Perognathoides*. The two teeth here described are, however, clearly heteromyines, and seem clearly to be referable to *Diprionomys*. They are the right size to belong only to *D. parvus* among described species, and cannot at the present time be separated from that species, even though the type is appreciably later (Thousand Creek).

The measurements of these specimens are as follows:

	antero-posterior	width anterior crest	width, posterior crest
M.C.Z. No. 8535, RP^4	1.40	0.77	1.43
M.C.Z. No. 8536, RM_2	1.02	1.27	1.23

SUMMARY

A small collection of Pliocene mammals, from the type locality of the Fish Lake Valley local fauna of Nevada, adds appreciably to our knowledge of that fauna. Included are: a talpid, *Domninoides; Hesperolagomys*, a new genus of ochotonid; a new species, *C. esmeraldensis*, of the cricetid *Copemys;* and the heteromyid

Diprionomys. The most abundant material, referable to the rabbit *Hypolagus fontinalis*, and the beaver *Eucastor dividerus*, adds to our knowledge of the dentition of these forms.

These materials permit a discussion of the interrelationships and evolutionary trends among Tertiary North American ochotonids and cricetids. *Hesperolagomys* is an unusually primitive Pliocene ochotonid, apparently representing the survival of a line derived from the primitive stock of the family, perhaps from *Desmatolagus*. The cricetid genus *Copemys* is revised, and three species previously included in *Peromyscus* are referred to it. Although cricetids are abundant in the middle Oligocene, the North American Miocene and Pliocene cricetids are largely limited to intermontane areas, with only two isolated teeth from the late Miocene Niobrara River local fauna of Nebraska and rare specimens from the Thomas Farm local fauna of Florida. They do not appear in numbers in the plains until the late Pliocene. Competition with entoptychine geomyids and with heteromyids may be the factors involved in the reduced numbers of cricetids in the Miocene and early Pliocene.

REFERENCES

BLACK, C. C.

1961a. Fossil mammals from Montana. Pt. I. Additions to the Late Miocene Flint Creek Local Fauna. Ann. Carnegie Mus., **36**: 69-76.

1961b. New rodents from the early Miocene deposits of Sixty-Six Mountain, Wyoming. Breviora, Mus. Comp. Zool., No. **146**: 1-7.

1961c. Rodents and lagomorphs from the Miocene Fort Logan and Deep River formations of Montana. Postilla, Yale Peabody Mus., No. **48**: 1-20.

BOHLIN, B.

1942. The fossil mammals from the Tertiary deposit of Taben-buluk, Western Kansu. Pt. I. Insectivora and Lagomorpha. Palaeont. Sinica, n.s. C, 8 a: 1-113.

BURKE, J. J.

1941. New fossil Leporidae from Mongolia. Amer. Mus. Novitates, No. **1117**: 1-23.

COPE, E. D.

1874. Notes on the Santa Fé marls and some of the contained vertebrate fossils. Proc. Acad. Nat. Sci. Phila., **26**: 147-152.

1875. Report on the geology of that part of northwestern New Mexico examined during the field season of 1874, by E. D. Cope, palaeontologist and geologist. Appendix LL, Ann. Rept. Chief of Engrs., Ann. Rept. Geogr. Expl. & Surv. West of 100th Meridian, Washington: 981-1036.

DAWSON, M. R.

1958. Later Tertiary Leporidae of North America. Univ. Kansas Paleont. Contrib., Vertebrata, **6**: 1-75.

FORSYTH MAJOR, C. I.

1899. On fossil and Recent Lagomorpha. Trans. Linn. Soc. London, (2), Zoology, **7**: 433-520.

GALBREATH, E. C.

1953. A contribution to the Tertiary geology and paleontology of northeastern Colorado. Univ. Kansas, Paleont. Contrib., Vertebrata, **4**: 1-120.

GREEN, M.

1956. The lower Pliocene Ogallala-Wolf Creek vertebrate fauna, South Dakota. Jour. Paleont., **30**: 146-169.

HALL, E. R.

1930a. A new genus of bat from the later Tertiary of Nevada. Univ. Calif. Publ., Bull. Dept. Geol. Sci., **19**: 319-320.

1930b. Rodents and lagomorphs from the Barstow beds of southern California. Univ. Calif. Publ., Bull. Dept. Geol. Sci., **19**: 313-318.

1930c. Rodents and lagomorphs from the later Tertiary of Fish Lake Valley, Nevada. Univ. Calif. Publ., Bull. Dept. Geol. Sci., **19**: 295-312.

HAY, O. P.

1902. Bibliography and catalogue of the fossil Vertebrata of North America. Bull. U.S. Geol. Surv., **179**: 1-868.

HOFFMEISTER, D. F.

1959. New cricetid rodents from the Niobrara River fauna, Nebraska. Jour. Paleont., **33**: 696-699.

HOOPER, E. T.

1957. Dental patterns in mice of the genus *Peromyscus*. Misc. Publ. Mus. Zool., U. Mich., **99**: 1-59.

MACINNES, D. G.

1953. The Miocene and Pleistocene Lagomorpha of East Africa. British Mus. (Nat. Hist.), Fossil Mamm. Africa, **6**: 1-30.

MCKENNA, M. C.

1960. The Geolabidinae. A new subfamily of early Cenozoic erinaceoid insectivores. Univ. Calif. Publ. Geol. Sci., **37**: 131-164.

MATTHEW, W. D.

1909. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. Mem. Amer. Mus. Nat. Hist., **9**: 291-567.

PATTERSON, B. and P. O. MCGREW

1937. A soricid and two erinaceids from the White River Oligocene. Geol. Ser. Field Mus. Nat. Hist., **6**: 245-272.

REED, K. M.

1960. Insectivores of the middle Miocene Split Rock local fauna, Wyoming. Breviora, Mus. Comp. Zool., No. **116**: 1-11.

STIRTON, R. A.

1935. A review of the Tertiary beavers. Univ. Calif. Publ., Bull. Dept. Geol. Sci., **23**: 391-458.

WHITE, T. E.

1954. Preliminary analysis of the fossil vertebrates of the Canyon Ferry reservoir site. Proc. U.S. Nat. Mus., **103** (3326): 395-438.

WOOD, A. E.

1935a. Evolution and relationships of the heteromyid rodents with new forms from the Tertiary of western North America. Ann. Carnegie Mus., **24**: 73-262.

1935b. Two new genera of cricetid rodents from the Miocene of western United States. Amer. Mus. Novitates, No. **789**: 1-3.

1936a. The cricetid rodents described by Leidy and Cope from the Tertiary of North America. Amer. Mus. Novitates, No. **822**: 1-8.

1936b. Fossil heteromyid rodents in the collections of the University of California. Amer. Jour. Sci., (5) **32**: 112-119.

1936c. Geomyid rodents from the middle Tertiary. Amer. Mus. Novitates, No. **886**: 1-31.

1937. The mammalian fauna of the White River Oligocene. Pt. II. Rodentia. Trans. Amer. Phil. Soc., n.s. **28**: 155-269.

1947. Miocene rodents from Florida. Bull. Mus. Comp. Zool., **99**: 489-494.

WOOD, A. E. and R. W. WILSON

1936. A suggested nomenclature for the cusps of the cheek teeth of rodents. Jour. Paleont., **10**: 388-391.

(Received December 1962)

ADDENDUM

Since this manuscript was completed, three papers, two dealing with Barstovian and Clarendonian, and one with Arikareean, cricetids have appeared. Shotwell (1963, p. 49) refers a lower jaw from the Clarendonian of eastern Oregon to *Peromyscus* cf. *dentalis*. James (1963, pp. 112-129) describes a considerable collection from the Clarendonian of the Cuyama area of California as *Peromyscus russelli,* and refers a single lower jaw from the Barstovian of the same area to *Peromyscus* aff. *dentalis*. Macdonald (1963, pp. 198-201) describes *Eumys blacki* and *E. woodi*, and lists *Scottimus,* sp. indet., from the Arikareean of South Dakota.

Shotwell's specimen is a jaw containing the first lower molar of an animal very similar to the type of *Copemys dentalis* (Fig. 8A). His figure (1963, fig. 52a) suggests an almost complete union of the anterolophid with the protoconid, which is incorrect, as there is a broad but shallow valley in this area, similar to that shown in Figure 8A. The metaconid is close to the anteroconid, also as in *C. dentalis*, to which this specimen clearly should be referred.

James' description of *Peromyscus russelli* indicates that it is very close to its contemporary, *Copemys esmeraldensis*, and that the two are certainly congeneric. The Cuyama form shows a union of the paracone of M^1 with both the anterior and posterior arms of the protocone, a condition more progressive than that seen in *C. esmeraldensis*. This type of union is present on $M^{2\text{-}3}$ as well (James, 1963, figs. 47, 52), and this species has thus progressed half way from the *Eumys* condition toward the situation in *Peromyscus*, where the union is exclusively through the anterior arm of the protocone. As in *Copemys*, the metacone of M^1 has shifted its point of attachment from the hypocone to the posteroloph, whereas this shift has not occurred in $M^{2\text{-}3}$. In the lower teeth, the pattern of M_3 is almost identical in the two populations (compare Fig. 9B and James, 1963, fig. 53a). In M_1, the California specimens show the same variation as to the presence or absence of the crest called the ectolophid by Hooper and by James (but *not* that called the ectolophid by Wood and Wilson). The peculiar accessory crests and cusps of the anteroconid region of *C. esmeraldensis* (Fig. 9C) do not seem to be present in the California species.

In spite of the similarity in pattern, there are significant distinctions in size, especially of the first molars. The length and width measurements of M^1 of M.C.Z. No. 7647 exceed those of the mean of *P. russelli* (James, 1963, Table 22) by about six times the standard deviation, and the length of the smaller M_1 of *C. esmeraldensis* exceeds that of *P. russelli* by over five times the standard deviation. The transverse diameter of M_1 of the larger Nevada specimen is larger by nearly 3.5 S.D. The third molar of M.C.Z. No. 7644 is larger than that of any specimen of *P. russelli*, but the difference is not significant. The probability that either measurement of M^1 or of M_1 of *C. esmeraldensis* falls within the limits of variation for the population of *P. russelli* is thus considerably less than .001, and is therefore negligible.

These factors all indicate that *Peromyscus russelli* should be referred to *Copemys*, and that *C. russelli* and *C. esmeraldensis* are closely related but distinct species.

The specimen referred by James to *Peromyscus* aff. *dentalis* is appreciably smaller than are the other specimens of *C. dentalis*, as James indicates (1963, p. 129), with an alveolar length of only 3.6 mm (cf. Table 4, where that of *C. dentalis* is given as 4.35-4.40 mm). It seems probable that this difference is great enough to place James' specimen outside the limits of *C. dentalis*. It is presumably also referable to *Copemys*.

Peromyscus parvus Sinclair (1905, p. 126) from the middle John Day of Oregon, was included by James as a rather distinctive species of *Peromyscus*, only questionably referable to the modern genus (1963, p. 128). Study of the only known specimen shows that it is clearly a small species of *Leidymys*.

In his paper on Arikareean fossils from South Dakota, Macdonald describes *Eumys blacki* (1963, p. 198, fig. 21), which is clearly congeneric with *Cotimus*, and *E. woodi* (*op. cit.*, p. 199, fig. 22), which is close to *E. eliensis*. He also refers two isolated upper molars to *Scottimus* sp. indet., thus extending the range of this genus into the Arikareean.

ADDITIONAL REFERENCES

JAMES, G. T.

1963. Paleontology and nonmarine stratigraphy of the Cuyama Badlands, California. Part 1. Geology, faunal interpretations and systematic descriptions of Chiroptera, Insectivora and Rodentia. Univ. Calif. Publ. Geol. Sci., **45**: 1-154.

MACDONALD, J. R.

1963. The Miocene faunas from the Wounded Knee area of western South Dakota. Bull. Amer. Mus. Nat. Hist., **125**: 139-238.

SHOTWELL, J. A.

1963. The Juntura Basin: studies in earth history and paleoecology. Trans. Amer. Phil. Soc., n.s. **53**: 1-77.

SINCLAIR, W. J.

1905. New or imperfectly known rodents and ungulates from the John Day series. Univ. Calif. Publ., Bull. Dept. Geol., **4**: 125-143.

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 3

AMERICAN SPIDERS OF THE GENUS *PHORONCIDIA* (ARANEAE: THERIDIIDAE)

By Herbert W. Levi

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
April 30, 1964

PUBLICATIONS ISSUED BY OR IN CONNECTION WITH THE

MUSEUM OF COMPARATIVE ZOOLOGY

HARVARD UNIVERSITY

BULLETIN (octavo) 1863 — The current volume is Vol. 131.

BREVIORA (octavo) 1952 — No. 203 is current.

MEMOIRS (quarto) 1864–1938 — Publication terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 41 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 28 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained from the Publications Office of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Peters' Check-List of Birds of the World. Volumes 1, 4 and 6 are out of print; volumes 2, 3, 5, 7, 9, 10 and 15 are currently available.

Phylogeny and Evolution of Crustacea. Proceedings of a conference held at Cambridge, Mass., March 6-8, 1962. H. B. Whittington and W. D. I. Rolfe, editors. Cambridge, Mass., 192 pp., 80 figs., 1963. Cloth bound, $6.75.

Fishes of the Gulf of Maine, by Henry B. Bigelow and William C. Schroeder. Washington, viii - 577 pp., 1953. Photo-offset reprint, $6.50.

PUBLICATIONS OF THE BOSTON SOCIETY OF NATURAL HISTORY

The remaining stock of the scientific periodicals of the Boston Society of Natural History has been transferred to the Museum of Comparative Zoology for distribution. Prices for individual numbers may be had upon request.

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 3

AMERICAN SPIDERS OF THE GENUS *PHORONCIDIA* (ARANEAE: THERIDIIDAE)

By Herbert W. Levi

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM

April, 1964

Bull. Mus. Comp. Zool., Harvard Univ., **131** (3): 65-86, April, 1964

No. 3 — *American Spiders of the Genus Phoroncidia* (*Araneae: Theridiidae*)

By Herbert W. Levi

Phoroncidia are mostly small spiders with the abdomen hard and sclerotized but of various shapes. The diversity in shape has caused arachnologists to assign different species to separate genera. Thus the synonymy of generic names (Levi and Levi, 1962) is long. Some species are similar to those placed in *Dipoena* (Hickman, 1951). However *Dipoena* females always have four seminal receptacles. while *Phoroncidia* have two. In *Dipoena* males, if the palpal embolus is long it curls counterclockwise in the left palpus; in *Phoroncidia*, the direction is the reverse. It is believed that the similarities, heavy sclerotization of the abdomen (only some species of *Dipoena*), projecting eye region of the carapace, and the relatively long fourth leg, have independently evolved. Nothing is known of the natural history of *Phoroncidia* species.

The Central and South American *P. tricuspidata* group, having three spines on the abdomen (Figs. 50, 56), is closest to its African relatives, some of which have five spines on the abdomen: two anteriorly, as in the American species, and three posteriorly. The commonest species is the North American *P. americana*, closely allied in shape and appearance to the European *P. paradoxa* (Lucas), and the Japanese *P. pilula* (Karsch); most other species are very rare. Almost half the specimens available were collected during the nineteenth century and these old specimens, collected by entomologists, are often in poor condition, having been speared on insect pins. The scarcity of specimens, and the abundance of species, make it difficult to match sexes. The paper thus reports only our very incomplete knowledge of the American species. Despite this, I have resisted the temptation of quoting unsupported literature records. I have not been able to examine the Mello-Leitão collection to verify his many records of *P. tricuspidata*. I suspect many are misidentified.

This paper, along with my others on American theridiid spiders, would not have been possible without the help of numerous colleagues who made rare specimens available. I extend sincerest thanks to Prof. M. Vachon of the Muséum National d' Histoire Naturelle, Paris (MNHN), Dr. A. Collart and Mr. J.

Kekenbosch of the Institut Royal des Sciences Naturelles de Belgique (ISNB), Dr. L. Brundin of the Natural History Museum Stockholm (RMS), Prof. G. C. Varley and Mr. E. Taylor of the Hope Department of Entomology, Oxford University, Dr. G. Owen Evans, Mr. K. Hyatt and Mr. D. Clark of the British Museum (Natural History) (BMNH); Dr. W. J. Gertsch of the American Museum of Natural History (AMNH), Dr. O. Kraus of the Senckenberg Museum (SMF), and Mr. W. Starega of the Polish Academy of Sciences, Warsaw. Dr. P. E. Vanzolini and his colleagues of the Departamento de Zoologia, São Paulo, provided locality information. Fr. Chrysanthus checked the latinization of specific names. The examination of types in European museums was made possible by a National Science Foundation Grant (G-4317), and the completion of the revision by a grant from the National Institutes of Health (AI-01944).

PHORONCIDIA Westwood

Phoroncidia Westwood, 1835, Zool. Jour., 5: 452. Type species by monotypy: *P. aculeata* Westwood, 1835, *ibid.*, 5: 453, tab. 22, fig. 9, ♀,♂ from Malaya.

Note. It is not known whether Westwood's specimens still exist. Only a few specimens determined by Berland in the Paris museum were examined. We recently published the synonymies (Levi and Levi, 1962).

Diagnosis. Theridiid spiders with colulus replaced by two setae, usually hidden underneath a sclerotized ring surrounding spinnerets. Carapace with eye region projecting above clypeus. Small chelicerae. Legs very short; fourth leg usually longer than first. Abdomen of various shapes, heavily sclerotized, often leathery, folded or with strong spines, humps, tubercles or extensions.

Epigynum a heavily sclerotized plate with openings, often indistinct, in the center or on the posterior border. Juvenile specimens may also have the epigastric area sclerotized. Only examination for the presence of seminal receptacles will determine whether the specimen is mature. The palpus usually has a paracymbial hook on or near the edge of the cymbium and the median apophysis probably does not touch the hook.

Distribution. Species are found in all parts of the world except northern Europe and western North America.

Misplaced species. Heribertus flavomaculatus Keyserling, 1891, Die Spinnen Amerikas, Theridiidae, 2(1): 223. *Ulesanis* *flavomaculata*, — Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., 29: 214 = *Dipoena flavomaculata* (Keyserling) [not "*Umfila flavomaculata*, — Petrunkevitch," Levi, 1963, Bull. Mus. Comp. Zool., 129: 151, a misprint].

Tricantha albopunctata Taczanowski, 1879, Horae Soc. Ent. Rossicae, 15: 123, pl. 2, fig. 36 = *Araneus albopunctatus* (Taczanowski), ARGIOPIDAE.

KEY TO AMERICAN PHORONCIDIA

1a. Abdomen with spines, humps, tubercles or projections 5
1b. Abdomen without spines, humps, tubercles or projections 2
2a. Dorsum of abdomen with many trapezoidal plates (Fig. 11); Amazon . . . *studo*
2b. Dorsum of abdomen covered by one single plate 3
3a. Trapezoidal impressions on dorsal plate (Fig. 17); Lower Amazon *longiceps*
3b. Dorsal plate without trapezoidal impressions .4
4a. Lateral eyes on tubercles (Fig. 2); Peru . . . . *moyobamba*
4b. Lateral eyes not on tubercles (Fig. 23); Est. Rio de Janeiro *rubromaculata*
5a. Abdomen subcircular in outline in dorsal view (Fig. 20) 6
5b. Abdomen trapezoidal, subtriangular or squarish with posterior projections 7
6a. Abdomen with only a median dorsal hump (Fig. 20); Chile . . *scutula*
6b. Abdomen with a median dorsal hump and paired humps posteriorly (Levi, 1955, figs. 7, 8); eastern Canada, eastern United States, Cuba, Jamaica . . *americana*
7a. Abdomen widest anteriorly and with a median dorsal posterior spine (Figs. 29, 45, 56) 11
7b. Abdomen as wide anteriorly as posteriorly, or wider posteriorly than anteriorly, usually without median posterior spine 8
8a. Abdomen trapezoidal in dorsal view with five dorsal spines (Figs. 36, 37); Minas Gerais *tina*
8b. Abdomen otherwise 9
9a. Abdomen with sides tuberculate and wrinkled (Figs. 32, 34); Chile *margamarga*
9b. Abdomen with at most median dorsal tubercles; with sclerotized plates 10
10a. Abdomen with longitudinal row of dorsal tubercles (Figs. 40, 41); Chile . . . . . *coquimbo*
10b. Abdomen with sclerotized spots but without tubercles (Figs. 25, 26); Chile . . . *nicoleti*
11a. Median posterior dorsal spine longer than anterior spines (Fig. 45) 12
11b. Three spines subequal in length 13

12a. Innumerable dorsal circular plates of abdomen almost touching (Fig. 29); Venezuela .... *ravot*

12b. Fourteen dorsal circular plates, far apart (Fig. 45); Peru .... *scutellata*

13a. Epigynum with a distinct median opening (Fig. 78); Est. São Paulo to Est. Rio Grande do Sul .... *reimoseri*

13b. Epigynum otherwise 14

14a. Epigynum with a V-shaped depression anterior to and between two dark spots containing openings (Fig. 73); Colombia .... *saboya*

14b. Epigynum otherwise 15

15a. Epigynum with paired openings near posterior margin (Fig. 58); Peru .... *flavolimbata*

15b. Epigynum otherwise 16

16a. Openings of epigynum indistinct lateral slits (Fig. 47); Est. Guanabara, Rio de Janeiro .... *tricuspidata*

16b. Epigynum otherwise 17

17a. Epigynum with a pair of distinct openings in a flat plate, anterior to a transverse keel (Fig. 63); southern Mexico, Central America .... *triunfo*

17b. Epigynum otherwise 18

18a. Epigynum with a median depression containing openings 19

18b. Epigynum without median depression, openings a pair of slits (Fig. 68); Minas Gerais .... *biocellata*

19a. Spines relatively short (Fig. 56); distinct pair of openings in depression of epigynum (Fig. 53); Paraguay .... *cribrata*

19b. Spines relatively long (Fig. 86); openings in epigynum depression indistinct (Fig. 83); Venezuela .... *gira*

PHORONCIDIA MOYOBAMBA sp. n.

Figures 1-5

Wibrada longiceps,—Archer, 1950, Paper Alabama Mus. Nat. Hist., no. 30: 27, pl. 4, fig. 4, ♂. Not *Wibrada longiceps* Keyserling.

Type. Male holotype from Moyobamba, San Martín, Peru, 20 Dec. 1946 (J. C. Pallister), in the American Museum of Natural History. The name is a noun in apposition after the type locality.

Description. Carapace, sternum dark brown; legs lighter brown. Abdomen, dorsum shiny brown; venter brown with a white spot on each side of pedicel, a white mark behind epigastric groove, brown ring around spinnerets, and a small white mark on each side of ring around spinnerets. Sides and clypeus of carapace punctate, dorsum almost smooth. Median eyes on stalk; lateral eyes on tubercles (Fig. 2). Anterior median eyes larger than others, slightly less than a diameter apart. Posterior median eyes one and one-half diameters apart. Sternum punctate. Dorsum of abdomen heavily sclerotized, domed, with paired slight depressions; venter folded with many sclerites (Figs. 3-5). Total length 1.6 mm. Carapace 0.8 mm long, 0.6 mm wide. First patella and tibia, 0.4 mm; second, 0.3 mm; third, 0.3 mm. Fourth femur, 0.4 mm; patella and tibia, 0.5 mm; metatarsus, 0.2 mm; tarsus, 0.2 mm.

Diagnosis. The shape of the carapace (Fig. 2) and color of the abdomen separate *P. moyobamba* from *P. rubromaculata.* The palpus (Fig. 1) has a shorter embolus than *P. longiceps.* The palpus resembles that of some species of *Dipoena,* but only determination of the number of female seminal receptacles will make the generic affiliation certain.

PHORONCIDIA STUDO sp. n.

Figures 6-11

Type. Female holotype from São Paulo de Olivença, Amazonas, Brazil (M. de Mathan), in the Muséum National d'Histoire Naturelle, Paris (No. 8329). The specific name is an arbitrary combination of letters.

Description. Carapace dark brown with posterior central portion lighter brown; sternum, legs dark brown. Abdomen dark brown, sclerites darker, a white pigment ring around lateral edge on venter (Figs. 9, 10), and some white pigment spots behind epigynum. Carapace tuberculate on sides. Median eyes on projection and each two lateral eyes on a tubercle (Fig. 6). Anterior median eyes slightly larger than others, their diameter apart. Posterior median eyes their diameter apart. Dorsum of abdomen with trapezoidal sclerites, venter also with sclerites (Figs. 9-11). Most sclerites with darker spot in middle and double bordered. Total length 2.1 mm. Carapace 0.9 mm long, 0.7 mm wide. First patella and tibia 0.5 mm; second 0.4 mm; third, 0.4 mm. Fourth femur, 0.6 mm; patella and tibia, 0.6 mm; metatarsus, 0.3 mm; tarsus, 0.3 mm.

Diagnosis. The unusual shape and arrangement of the sclerotized plates readily separate this species from all other *Phoroncidia.* I suspect that this is the female of *Phoroncidia longiceps,* known only from a male. A juvenile male collected in Peru has its abdomen like that of the female but the median eye region projects farther anteriorly.

Records. Peru. Huánuco: Divisoria, Sept., Oct. 1946, 1 juv. ♂ (F. Woytkowski, AMNH). *Brazil. Amazonas.* São Paulo de Olivença, ♀ paratype (M. de Mathan, MNHN).

PHORONCIDIA LONGICEPS (Keyserling), n. comb.

Figures 12-17

Wibrada longiceps Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, 2(2): 22, pl. 11, fig. 145, ♂. Male holotype from "Peru," in the Muséum National d'Histoire Naturelle, Paris, examined.

Vibrada longiceps, — Simon, 1894, Histoire Naturelle des Araignées, 1: 560, fig. 570.

Note. Keyserling's locality is in error since the specimen is marked as coming from Le Para [Belém, Brazil] and was collected by M. de Mathan. Simon (1894) indicated that the specimen came from the Amazon region of Brazil. Keyserling apparently misread Peru for Para on the label.

Description. Carapace dark brown, the portion covered by abdomen lighter. Sternum, legs dark brown. Dorsum of abdomen dark brown; venter with sclerotized areas dark brown but a ring of white pigment between dorsal and ventral scuta (Figs. 15, 16). Carapace tuberculate on sides; sternum tuberculate. Anterior median eyes slightly larger than others, their diameter apart. Posterior median eyes their diameter apart. Median eyes projecting (Figs. 12, 13), and laterals on a hump. Chelicerae with small fangs. Abdomen with a dark dorsal shield that has impressions of trapezoids; in the center of each is a dark spot (Figs. 15, 17). Total length 1.6 mm. Carapace 0.9 mm long, 0.7 mm wide. First patella and tibia, 0.4 mm; second, 0.3 mm; third, 0.3 mm. Fourth femur, 0.5 mm; patella and tibia, 0.5 mm; metatarsus, 0.2 mm; tarsus, 0.2 mm.

Judging by the trapezoid dorsal impressions and the trapezoid plates on dorsum of the abdomen, *P. studo* may be the female of *P. longiceps*.

PHORONCIDIA RUBROMACULATA (Keyserling), n. comb.

Figures 21-23

Heribertus rubromaculatus Keyserling, 1886, Die Spinnen Amerikas, Theridiidae, 2(2): 28, pl. 11, fig. 148, ♂. Fragments of male type from [Nova Friburgo, Est. Rio de Janeiro] Brazil, in the Muséum National d'Histoire Naturelle, Paris, examined.

Ulesanis rubromaculata, — Simon, 1894, Histoire naturelle des Araignées, 1: 554.

Note. Keyserling described the species from "Brazil." The label in the type vial indicates that the specimen came from "N. Friburgo." Both palpi and most legs of the holotype are missing.

Description. Carapace dark brown. Sternum, legs brown. Sclerotized part of abdomen brown, dorsum with a median white mark, which is longer than wide and was probably reddish in the live spider (Fig. 23). Eyes subequal in size. Anterior median eyes one and one-half diameters apart, two and one-half diameters from laterals. Posterior median eyes one and one-half diameters apart, one and three-quarters diameters from laterals. Eye region of carapace high and projecting anteriorly (Fig. 21). Abdomen with heavily sclerotized dorsal shield having some darker marks. Venter with numerous sclerotized areas (Figs. 21, 22). Total length 2.1 mm. Carapace 1.0 mm long, 0.8 mm wide. First femur, 0.7 mm. Second patella and tibia, 0.5 mm.

Phoroncidia scutula (Nicolet), n. comb.

Figures 18-20

Gasteracantha scutula Nicolet, 1849, *in* Gay, Historia de Chile, Zool., 10(3): 478, pl. 5, fig. 6, ♀. Female type from Chile lost.

Gasteracantha caduceator Nicolet, 1849, *op. cit.*, p. 479. Female type from Chile, lost.

Gasteracantha violaceata Nicolet, 1849, *op. cit.*, p. 479. Female type from Chile, lost.

Gasteracantha porcellanae Nicolet, 1849, *op. cit.*, p. 480. Female type from Chile, lost.

Gasteracantha maculata Nicolet, 1849, *op. cit.*, p. 480. Female type from Chile, lost.

Gasteracantha venusta Nicolet, 1849, *op, cit.*, p. 480. Female type from Chile, lost.

Gasteracantha ventrosa Nicolet, 1849, *op. cit.*, p. 481. Female type from Chile, lost.

Gasteracantha scitula Nicolet, 1849, *op. cit.*, p. 481. Female type from Chile, lost.

Gasteracantha inflata Nicolet, 1849, *op. cit.*, p. 482. Female type from Chile, lost.

Gasteracantha columnata Nicolet, 1849, *op. cit.*, p. 482. Female type from Chile, lost.

Gasteracantha punctata Nicolet, 1849, *op. cit.*, p. 483. Female type from Chile, lost.

Gasteracantha minuta Nicolet, 1849, *op. cit.*, p. 483. Female type from Chile, lost.

Ulesanis scutula, — Keyserling, 1886, Die Spinnen Amerikas, Theridiidae. 2(2): 18, pl. 11, fig. 14, ♀. — Tullgren, 1902, Bih. Svenska Vet. Akad. Handl., 28(4): 16, fig. 5, ♂. Bonnet, 1959, Bibliographia Araneorum, 2:4753.

Note. Keyserling first synonymized Nicolet's *Gasteracantha* species. According to Keyserling the abdomen of the female is like that of the male.

Description. Male. Carapace dark grayish brown. Distal end of labium and maxillae white. Sternum dark gray-brown. Legs dark brown except coxae and tarsi white. Abdomen black with white spots on dorsum or sides, no two specimens alike. Sclerotized parts very dark brown. Carapace highest in thoracic region (Fig. 19). Anterior median eyes slightly larger than others, their diameter apart and one diameter from laterals. Posterior median eyes two-thirds diameter apart, one and one-quarter diameters from laterals. Abdomen dorsum covered by a sclerotized, punctate scutum, with a dorsal hump (Figs. 19, 20). Sclerotized plates and spots on sides; epigastric area heavily sclerotized and sclerotized ring around spinnerets. Total length 1.8 mm. Carapace 0.9 mm long, 0.8 mm wide, 0.4 mm high. First patella and tibia, 0.6 mm; second, 0.5 mm; third, 0.4 mm. Fourth femur, 0.6 mm; patella and tibia, 0.7 mm; metatarsus, 0.3 mm; tarsus, 0.3 mm.

Older males have the abdomen more wrinkled ventrally than younger ones.

Records. Bolivia. Bení: Rurrenabaque, 10 Nov. 1956, ♂ (L. Peña, ISNB). *Chile. Valdivia:* Enco, 3 March 1955, ♂ (L. Peña, ISNB). *Llanquihue:* Carelmapu, 21-28 Feb. 1961, ♂ (L. Peña, ISNB). *Aysen:* Upper part of Aysen Valley, ♂ (P. Dusen, RMS).

PHORONCIDIA AMERICANA (Emerton)

Map

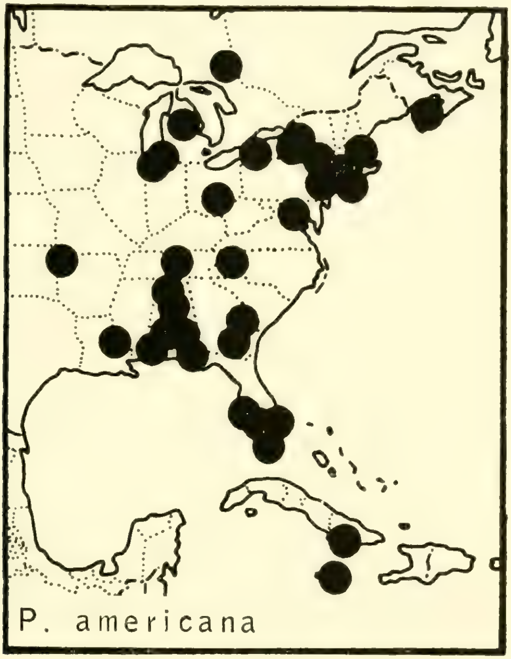
Ulesanis americana Emerton, 1882, Trans. Connecticut Acad. Sci., 6: 28, pl. 6, fig. 1, ♀, ♂. Female, male syntypes from New Haven, Connecticut, in the Museum of Comparative Zoology, examined. — Bonnet, 1959, Bibliographia Araneorum, 2:4751.

Oronota americana, — Levi, 1955, Ann. Ent. Soc. Amer., 48; 334, figs. 1-8, ♀, ♂.

Distribution. Eastern Canada, eastern United States, Cuba, Jamaica. (Map.)

Additional Records. Canada. Nova Scotia: Coldbrook, 31 Aug. 1955 (C. Dondale). *Ontario.* Marten River, 36 mi. N of North Bay, 31 Aug. 1955 (H., L. Levi). *United States. Michigan.* Crawford Co.: Hartwick Pines, Sept. 1955 (H., L. Levi).

Arkansas. Washington Co.: Cove Creek Valley, 15 mi. W of Prairie Grove; Boston Mts., 300 m (O. Hite). *Jamaica:* Hardwar Gap, 5 Dec. 1954, ♂ (A. M. Nadler, AMNH).



Distribution of *Phoroncidia americana.*

PHORONCIDIA NICOLETI sp. n.

Figures 24-26

Type. Male holotype from Sierra de Chillán, Chillán, Chile, in the Muséum National d'Histoire Naturelle, Paris (no. 17699). The species is named after the early French arachnologist H. Nicolet.

Description. Carapace brown with indistinct gray marks radiating to sides. Sternum brown. Legs brown with distal segments lighter. Abdomen dark gray with a narrow dorsal light crescent, underlain by white pigment, with its arms pointing posteriorly (Fig. 26). Ring around spinnerets darker gray. Carapace only slightly overhanging eye region. Eyes subequal in size. Anterior eyes their diameter apart. Posterior medians one and one-quarter diameters apart, two-thirds diameter from laterals. Abdomen with two posterior pointing projections (Figs. 25, 26), corniculate, except for smooth area of white crescent. Total length 1.6 mm. Carapace 0.7 mm long, 0.7 mm wide. First femur, 0.7 mm; patella and tibia, 0.6 mm; metatarsus, 0.4 mm; tarsus, 0.3 mm. Second patella and tibia, 0.5 mm; third, 0.4 mm; fourth, 0.6 mm.

Diagnosis. The two projections of the abdomen (Figs. 25, 26) distinguish this species from *P. scutula*, and the lack of dorsal tubercles from *P. coquimo*.

PHORONCIDIA RAVOT sp. n.

Figures 27-29

Type. Male holotype from Tovar, Aragua, Venezuela, 1888 (E. Simon), in the Muséum National d'Histoire Naturelle, Paris (no. 10171). The specific name is a noun in apposition, an anagram of the type locality.

Description. Carapace dark brown, sternum brown, legs yellow-brown. Abdomen dark brown except for two pairs of white spots on dorsum, a large white patch on each side above spinnerets, and a white patch on each side of the venter anterior to pedicel above carapace. Carapace with median eyes on projection and laterals on a slight hump. Eyes subequal in size. Anterior median eyes one diameter apart. Posterior median eyes one and one-half diameters apart, about three diameters from posterior laterals. Abdomen subtriangular with a median dorsal posterior spine (Figs. 27, 29). Dorsum covered with innumerable small sclerotized discs; some elongate plates on ventral part of sides and venter with some round plates and spots between epigastric groove and sclerotized ring surrounding spinnerets. Total length 2.0 mm. Carapace 1.0 mm long, 0.8 mm wide. First patella and tibia, 0.6 mm; second, 0.4 mm; third, 0.4 mm. Fourth femur, 0.6 mm; patella and tibia, 0.6 mm; metatarsus, 0.3 mm; tarsus, 0.3 mm.

Diagnosis. The well-sclerotized palpus has the embolus almost straight, unlike any other *Phoroncidia* examined (Fig. 28). It is possible that this is the male of *P. gira* collected at the same locality, and having a triangular abdomen.

Records. Venezuela. Aragua: Tovar, 2 juv. paratypes, 1888 (E. Simon, MNHN).

PHORONCIDIA MARGAMARGA sp. n.

Figures 30-34

Type. Female holotype from Marga Marga, Valparaiso Prov., Chile, 11-13 Sept. 1954 (L. Peña), in the Institut Royal des Sciences Naturelles de Belgique, Brussels. The specific name is a noun in apposition after the type locality.

Description. Carapace dark brown, eye region yellowish white. Chelicerae, sternum yellow-white. Legs yellow-white, except fourth femur with a distal brown ring; all tibiae with a distal dark brown ring. Abdomen with scattered gray and black pigment, sclerotized spots over muscle attachment black, and two longitudinal parallel lines of black pigment spots (Fig. 34). Venter of abdomen with scattered gray pigment and three black spots on each side of sclerotized ring around spinnerets. Eyes subequal in size, anterior medians slightly less than their diameter apart, and slightly less than their diameter from laterals. Posterior median eyes one-third diameter apart, one and one-half diameters from laterals. Abdomen wrinkled and with humps (Figs. 32-34). Total length of female 2.7 mm. Carapace 0.6 mm long, 0.8 mm wide. First patella and tibia, 0.7 mm; second, 0.6 mm; third, 0.6 mm. Fourth femur, 0.9 mm; patella and tibia, 0.9 mm; metatarsus, 0.5 mm; tarsus, 0.4 mm.

Diagnosis. The abdomen shape (Figs. 32-34) distinguishes this species from other *Phoroncidia.* The epigynum shows no noticeable structure. The lateral dark spots are muscle attachments. The internal ducts are so transparent that they were invisible on the single specimen examined. The indistinct opening, however, seems to be in the center.

PHORONCIDIA COQUIMBO sp. n.

Figures 38-41

Type. Female holotype from Hacienda Illapel, 600-1300 m elev., Coquimbo, Chile, 24-31 Oct. 1954 (L. Peña), in the Institut Royal des Sciences Naturelles de Belgique, Brussels. The specific name is a noun in apposition after the province of the type locality.

Description. Carapace dark brown, lighter in middle and behind. Sternum brown with a narrow darker border. Legs yellow-brown, proximal end and distal half of femora, patellae and distal half of tibiae brown. Abdomen reddish brown, black on each side, some black pigment across middle and on lateral extensions; white pigment spots around each nipple and on dorsum of each lateral extension. Venter reddish brown, darker around spinnerets; a white spot on each side of the epigastric area (Figs. 40, 41). Eyes subequal in size. Anterior median eyes two-thirds diameter apart, three-quarters diameter from laterals. Posterior median eyes three-quarters diameter apart, one and one-quarter diameters from laterals. Abdomen wider than long with four dorsal nipples in a longitudinal row and two lateral posterior extensions (Fig. 41), many small sclerotized discs and numerous small sclerotized spots all over abdomen. Sclerotized ring around spinnerets. Total length 3.0 mm. Carapace 0.8 mm long, 0.9 mm wide. First patella and tibia, 0.6 mm; second, 0.6 mm; third, 0.5 mm. Fourth femur, 0.8 mm; patella and tibia, 0.8 mm; metatarsus, 0.4 mm; tarsus, 0.3 mm.

Diagnosis. The sclerotization of the abdomen is lighter than in other species of *Phoroncidia.* The shape of the abdomen (Figs. 40, 41) is distinct. The epigynum has an indistinct median opening (Fig. 39); the two seminal receptacles are spherical (Fig. 38). The course of the ducts remains uncertain.

PHORONCIDIA TINA sp. n.

Figures 35-37

Type. Male holotype from Diamantina, Minas Gerais, Brazil, 1902 (E. Gounelle) in the Muséum National d'Histoire Naturelle, Paris (no. 22462). The specific name is an arbitrary combination of letters.

Description. Carapace yellow with a median thin longitudinal black line; area between eyes black. Sternum yellow. Legs yellow; fourth darkest, brownish. Abdomen dorsum silver with sclerotized discs yellow, giving it a golden appearance. Sides of abdomen silver; venter black except for silver spot between epigastric groove and dark ring around spinnerets. Carapace with eye region projecting (Fig. 36). Anterior median eyes larger than other eyes, one-third their diameter apart, almost touching laterals. Posterior eyes less than their diameter apart. Abdomen with five dorsal thorns (Figs. 36, 37). First leg with spines on ventral tibia and one on distal end of metatarsus. Sclerites of palpus weakly sclerotized. Total length 2.1 mm. Carapace 0.9 mm long, 0.9 mm wide. First femur, 1.1 mm; patella and tibia, 0.9 mm; metatarsus, 0.5 mm; tarsus, 0.4 mm. Second patella and tibia, 0.7 mm; third, 0.5 mm; fourth, 1.0 mm.

Diagnosis. This is the only American species of *Phoroncidia* having five dorsal spines (Figs. 36, 37). This specimen was in the vial with two female *P. biocellata*, but is believed to be a separate species.

PHORONCIDIA SCUTELLATA (Taczanowski), n. comb.

Figures 42-45

Tricantha scutellata Taczanowski, (1879) 1880, Horae Soc. Ent. Rossicae, 15: 122, pl. 1, fig. 35. Female holotype from Amable María, [prov. Tarma, Junín], Peru, in the Polish Academy of Sciences, Warsaw, examined.

Description. Carapace yellow-brown, head region lighter, sternum, legs yellow-brown. Abdomen with white pigment on dorsum; tip of posterior spine orange and sclerotized discs brown. Sides of venter with white pigment, most of venter bare of pigment, sclerotized areas brown. Eyes subequal in size. Anterior median eyes one diameter apart, one and one-half diameters from laterals. Posterior median eyes a little more than their diameter apart, almost two diameters from laterals. Sternum slightly punctate. Abdomen relatively small, shield-shaped with a median dorsal posterior spine (Figs. 44, 45). Total length 2.5 mm. Carapace 1.0 mm long, 1.1 mm wide. First patella and tibia, 0.8 mm; second, 0.6 mm; third, 0.6 mm. Fourth femur, 0.9 mm; patella and tibia, 1.0 mm; metatarsus, 0.5 mm; tarsus, 0.4 mm.

PHORONCIDIA CRIBRATA (Simon), n. comb.

Figures 52-56

Trithena cribrata Simon, 1893, Ann. Soc. ent. France, 62: 323, pl. 7, fig. 5. ♀. Female holotype from Paraguay in the Muséum National d'Histoire Naturelle, Paris, examined.

Description. Carapace brown, darker on sides; sternum yellow-brown. Legs yellow-brown, fourth darkest. Abdomen white except for an unpigmented area on each side of pedicel (Fig. 55), three orange to dark brown spines, large dark brown and smaller brown sclerotized spots, and dark brown epigynum and spinneret area. Eyes subequal in size. Anterior median eye one diameter apart, one and one-third diameters from laterals Posterior median eyes one diameter apart, two diameters fro laterals. Abdomen with three spines but more spherical in shap than related species, and with many small sclerotized spot

(Figs. 54-56). Total length 4.9 mm. Carapace 1.3 mm long, 1.1 mm wide. First patella and tibia, 0.9 mm; second, 0.7 mm; third, 0.7 mm. Fourth femur, 1.1 mm; patella and tibia, 1.2 mm; metatarsus, 0.4 mm; tarsus, 0.4 mm.

Diagnosis. The epigynum has two separate openings in a common, central, heavily sclerotized depression (Fig. 53). The spines are shorter than those of related species.

PHORONCIDIA TRICUSPIDATA (Blackwall), n. comb.

Figures 46-51

Plectana tricuspidata Blackwall, 1863, Ann. Mag. Nat. Hist., (3) 11: 38. Female holotype from Rio de Janeiro, Brazil, in the Hope Department of Entomology, Oxford University, examined.

Tricantha tricornis Simon, 1864, Histoire Naturelle des Araignées, 1 edit., p. 293, fig. 136, ♀; *nomen nudum.* From Brazil.

Tricantha inuncans Simon, 1867, Rev. Mag. Zool., (2) 19: 23. Female holotype from Nova Friburgo, [Est. Rio de Janeiro], Brazil, in the Muséum National d'Histoire Naturelle, Paris, examined. This specimen has an insect pinhole through the epigynum.

Description. Female holotype of *P. tricuspidata:* carapace, sternum, legs yellow-brown. Dorsum of abdomen white, three spines orange. Both the type of *T. inuncans* and the specimen from Teresópolis without dorsal pigment. Venter of abdomen without pigment except for white on each side of pedicel and ringing spinnerets up to genital groove; an unpigmented streak up each spine. Eyes subequal in size, posterior median eyes slightly smaller than others. Anterior median eyes less than a diameter apart, one diameter from laterals. Posterior median eyes one diameter apart, two diameters from laterals. Chelicerae with two anterior teeth. Abdomen with three spines, dorsum with large round sclerotized plates of variable size (Figs. 50, 51), and some few small sclerotized spots. Epigynum with slits, very difficult to discern in most specimens (Fig. 47). Total length 5.5 mm. Carapace 1.4 mm long, 1.4 mm wide. First patella and tibia, 1.1 mm; second, 0.8 mm; third, 0.7 mm. Fourth femur, 1.2 mm; patella and tibia, 1.4 mm; metatarsus, 0.6 mm; tarsus, 0.5 mm.

The holotype of *T. inuncans* has larger paired dorsal discs (Fig. 51) than the holotype of *P. tricuspidata* (Fig. 50).

Records. Brazil. Est. Rio de Janeiro: Teresópolis, ♀ (MNHN); March 1946, ♀ (H. Sick, AMNH).

PHORONCIDIA FLAVOLIMBATA (Simon), n. comb.

Figures 57-61

Tricantha flavolimbata Simon, 1893, Ann. Soc. ent. France, 62: 322, pl. 7, fig. 3. Female holotype from Loja, Ecuador, in the Muséum National d'Histoire Naturelle, Paris, examined.

Description. Carapace yellow-brown, black in immediate area around anterior median eyes and between lateral eyes. Sternum dark brown; legs yellow. Abdomen white except for golden yellow spines, dark brown sclerotized spots, and minute scattered orange spots on dorsum. Epigynum dark brown and area around spinnerets also dark brown. Eyes subequal in size. Anterior median eyes one diameter apart, one and one-third diameters from laterals. Posterior eyes one and one-half diameters apart. Abdomen widest anteriorly with three spines, and having sclerotized spots on dorsum and venter (Figs. 59-61). Total length 5.9 mm. Carapace 1.2 mm long, 1.3 mm wide. First patella and tibia, 1.1 mm; second, 0.8 mm; third, 0.8 mm. Fourth femur, 1.3 mm; patella and tibia, 1.3 mm; metatarsus, 0.7 mm; tarsus, 0.5 mm.

Diagnosis. The epigynum has the openings near the posterior border, at the lateral ends of a transverse groove (Fig. 58).

PHORONCIDIA BIOCELLATA (Simon), n. comb.

Figures 67-71

Tricantha biocellata Simon, 1893, Ann. Soc. ent. France, 62: 323, pl. 7, fig. 4. Female lectotype here designated from Caraça, Minas Gerais, Brazil, in the Muséum National d'Histoire Naturelle, Paris, examined.

Description. Carapace, sternum, legs yellow-brown. Abdomen with less white pigment than in some related species (Fig. 71), spines orange to black. The paratype has more white pigment than the lectotype. The epigynum and the ring around spinnerets dark brown. Eyes subequal in size. Anterior median eyes slightly less than one diameter apart, slightly less than two diameters from laterals. Posterior median eyes one and one-quarter diameters apart. Two diameters from laterals. The paratype, although mature, is much smaller than the lectotype, being only 3.7 mm total length. Total length of lectotype 4.8 mm. Carapace 1.2 mm long, 1.1 mm wide. First patella and tibia, 1.0 mm; second, 0.6 mm; third, 0.6 mm. Fourth femur, 1.0 mm; patella and tibia, 1.2 mm; metatarsus, 0.6 mm; tarsus, 0.4 mm.

Diagnosis. Abdomen less sclerotized than in related species, having only large sclerotized discs but no small spots on dorsum (Figs. 69, 71). Epigynum openings are indistinct slits (Fig. 68); connecting ducts (Fig. 67) transparent.

Record. Brazil. Minas Gerais: Diamantina, 1902, 2♀ (E. Gounelle, MNHN); Caraça, ♀ paratype (E. Gounelle, MNHN).

PHORONCIDIA TRIUNFO sp. n.

Figures 62-65

Tricantha tricornis, — F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 540, pl. 51, fig. 26, ♀. Not *Tricantha tricornis* Simon.

Type. A damaged female holotype from El Triunfo, Chiapas, Mexico, 2000 m alt., April 1942 (H. Wagner), in the American Museum of Natural History. The specific name is a noun in apposition after the type locality.

Description. Carapace brown. Sternum lighter brown. Legs brown. Dorsum of abdomen white, sclerotized spots brown, three spines orange. Venter whitish with brown epigynum and ring around spinnerets. Eyes subequal in size; anterior median eyes one diameter apart, one and one-half diameters from laterals. Posterior median eyes one diameter apart, two diameters from laterals. Abdomen (Figs. 64, 65) with three spines, paired dorsal sclerotized discs and small sclerotized spots. Total length 4.6 mm. Carapace 1.3 mm long, 1.3 mm wide. First patella and tibia, 1.2 mm; second, 0.8 mm; third, 0.8 mm. Fourth femur, 1.3 mm; patella and tibia, 1.4 mm; metatarsus, 0.8 mm; tarsus, 0.5 mm.

Diagnosis. Epigynum, with two separate openings in a flat area anterior to a keel (Fig. 63), distinguishes this species from *P. tricuspidata* and *P. cribrata*.

Records. Mexico. Colima: Nevada de Colima, 21 Jan. 1943, juv. (F. Bonet, AMNH). *Chiapas:* El Triunfo, 2000 m, April 1942, fragments of 2 ♀ paratypes (H. Wagner, AMNH). *Guatemala.* Motaña de Chilasco (F. P.-Cambridge, 1902). *Costa Rica.* Tablazo, juv. (Tristan).

PHORONCIDIA SABOYA sp. n.

Figures 72-76

Type. Female holotype from "Cabin La Luzera," Saboyá, Boyacá, Colombia, in the British Museum. The specific name is a noun in apposition after the type locality.

Description. The type is in poor physical condition, having originally been pinned and dried. Carapace, sternum, legs yellow-brown. Abdomen with spines orange-white; sides and anterior of dorsum white and middle with scattered white pigment; sclerotized plates and smaller spots light brown. Venter with some scattered white pigment spots, sides white. Anterior median eyes very slightly larger than others, one and one-quarter diameters apart, two diameters from laterals. Posterior median eyes one and three-quarters diameters apart, two diameters from laterals. Abdomen (Figs. 74-76) with three large spines and dorsum with paired round plates and scattered smaller sclerotized spots. Spines less sclerotized than in related species. Total length 5.5 mm. Carapace 1.5 mm long, 1.8 mm wide. First patella and tibia, 1.4 mm; second, 1.2 mm; third, 1.1 mm. Fourth femur, 1.7 mm; patella and tibia, 1.4 mm; metatarsus, 0.9 mm; tarsus, 0.6 mm.

Diagnosis. The base of the abdominal spines is wider (Figs. 74-76) than in related species. The epigynum differs from *P. triunfo* and others by having two indistinct dark spots containing the openings, and between and anterior to the spots a deep V-shaped groove (Fig. 73).

PHORONCIDIA REIMOSERI sp. n.

Figures 77-81

Type. Female holotype from Est. Rio Grande do Sul, 1908, Brazil (E. Reimoser), in the Museum of Comparative Zoology. The species is named after its collector, the arachnologist E. Reimoser.

Description. Carapace, sternum shiny dark brown. Legs lighter brown, distal portion of fourth femora, and fourth patellae darker. Abdomen with spines shiny black, dorsum yellow-white in alcohol; venter white proximal to spines; sides and posterior black; a dark brown ring around spinnerets and white between. Anterior median eyes slightly larger than others; two-thirds diameter apart, two diameters from laterals. Posterior median eyes one and one-half diameters apart, two diameters from laterals. Abdomen with three spines (Figs. 79-81), sclerotized discs, and variable number of tiny sclerotized spots. Total length of females 3.3-5.0 mm. Total length of one female 4.6 mm. Carapace 1.3 mm long, 1.3 mm wide. First patella and tibia, 1.0 mm; second, 0.8 mm; third, 0.7 mm. Fourth femur, 1.1 mm; patella and tibia, 1.3 mm; metatarsus, 0.6 mm; tarsus, 0.5 mm.

Drawings were made from a recently collected specimen from Nova Teutonia.

Diagnosis. The single median opening in the epigynum (Fig. 78) distinguishes the species from *P. tricuspidata.*

Records. Brazil. Est. São Paulo: Fazienda Novo-Niagara, lat 23° 00′ S, long 49° 20′ W, 1898, ♀ (E. Gounelle, MNHN). *Santa Catarína:* Nova Teutonia, lat 27° 11′ S, long 52° 23′ W, ♀ (F. Plaumann, SMF).

PHORONCIDIA GIRA sp. n.

Figures 82-86

Type. Female holotype from Tovar, Aragua, Venezuela, 1888 (E. Simon) in the Muséum National d'Histoire Naturelle, Paris (no. 10025). The specific name is an arbitrary combination of letters.

Description. Carapace, sternum brown, legs lighter brown. Abdomen with three orange-colored spines, dorsum white except for dark brown sclerotized discs and spots; venter white on sides, but area between epigynum and spinnerets on sides of pedicel without pigment. Eyes subequal in size. Anterior median eyes one diameter apart, one and one-half diameters from laterals. Posterior median eyes one and one-quarter diameters apart, two diameters from laterals. Abdomen with three spines, large, dark discs and smaller sclerotized spots on dorsum and venter. Total length 5.7 mm. Carapace 1.3 mm long, 1.4 mm wide. First patella and tibia, 1.0 mm; second, 0.5 mm; third, 0.5 mm. Fourth femur, 1.3 mm; patella and tibia, 1.3 mm; metatarsus, 0.6 mm; tarsus, 0.5 mm.

Diagnosis. The epigynum has a posterior median dark depression with an indistinct dark spot in each side of it (Fig. 83). The region posterior to the depression is heavily sclerotized. The connecting ducts are hardly visible in the cleared female genitalia (Fig. 82). The structure on the epigynum and the relatively long abdominal spines separate the species from *P. triunfo* and *P. tricuspidata.*

REFERENCES

HICKMAN, V. V.

1951. New Phoroncidiinae and the affinities of the New Zealand spider *Atkinsonia nana* Cambridge. Papers Proc. Roy. Soc. Tasmania, 1950: 3-24.

LEVI, H. W.

1955. The spider genera *Oronota* and *Stemmops* in North America, Central America and the West Indies (Araneae, Theridiidae). Ann. Ent. Soc. America, **48**(5): 333-342.

LEVI, H. W. and L. R. LEVI

1962. The genera of the spider family Theridiidae. Bull. Mus. Comp. Zool., **127**(1): 1-71.

(Received May 13, 1963.)

INDEX

Valid names are printed in italics.

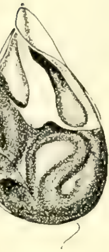
albopunctata, Tricantha, 69
americana, Oronota, 74
americana, Phoroncidia, 74
americana, Ulesanis, 74
biocellata Phoroncidia, 81
biocellata, Tricantha, 81
caduceator, Gasteracantha, 73
columnata, Gasteracantha, 73
coquimbo, Phoroncidia, 77
cribrata, Phoroncidia, 79
cribrata, Trithena, 79
flavolimbata, Phoroncidia, 81
flavolimbata, Tricantha, 81
flavomaculata, Ulesanis, 68
gira, Phoroncidia, 84
inflata, Gasteracantha, 73
inuncans, Tricantha, 80
longiceps, Phoroncidia, 72
longiceps, Wibrada, 70, 72
maculata, Gasteracantha, 73
margamarga, Phoroncidia, 77
minuta, Gasteracantha, 73
moyobamba, Phoroncidia, 70
nicoleti, Phoroncidia, 75
porcellanae, Gasteracantha, 73
punctata, Gasteracantha, 73
ravot, Phoroncidia, 76
reimoseri, Phoroncidia, 83
rubromaculata, Phoroncidia, 72
rubromaculata, Ulesanis, 72
saboya, Phoroncidia, 82
scitula, Gasteracantha, 73
scutellata, Phoroncidia, 79
scutellata, Tricantha, 79
scutula, Gasteracantha, 73
scutula, Phoroncidia, 73
scutula, Ulesanis, 73
studo, Phoroncidia, 71
tina, Phoroncidia, 78
tricornis, Tricantha, 80, 82
tricuspidata, Phoroncidia, 80
tricuspidata, Plectana, 80
triunfo, Phoroncidia, 82
ventrosa, Gasteracantha, 73
venusta, Gasteracantha, 73
violaceata, Gasteracantha, 73

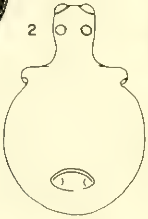
PLATES

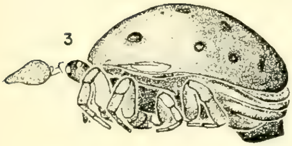
Figs. 1-5. *Phoroncidia moyobamba* sp. n., male. 1. Left palpus. 2. Carapace. 3. Lateral view. 4. Abdomen, ventral view. 5. Abdomen and carapace, dorsal view.

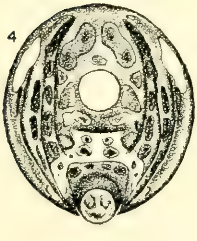
Figs. 6-11. *P. studo* sp. n., female. 6. Carapace. 7. Genitalia, dorsal view. 8. Epigynum. 9. Abdomen, ventral view. 10. Lateral view. 11. Carapace and abdomen, dorsal view.

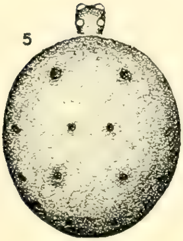
Figs. 12-17. *P. longiceps* (Keyserling), male. 12, 13. Carapace. 14. Palpus. 15. Lateral view. 16. Abdomen, ventral view. 17. Carapace and abdomen, dorsal view.

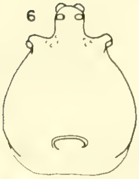
1


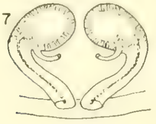
2


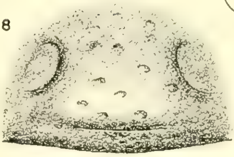
3


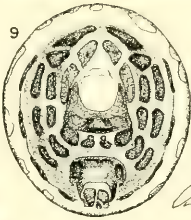
4


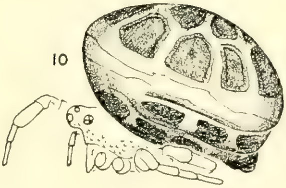
5


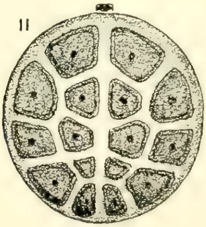
6


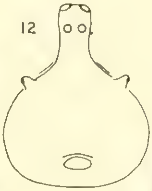
7


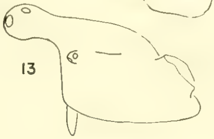
8


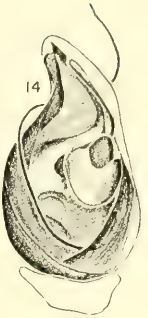
9


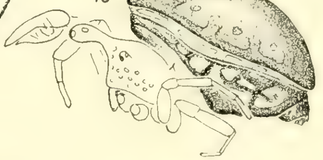
10


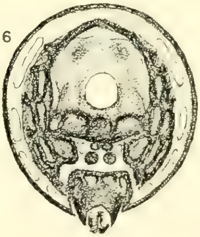
11


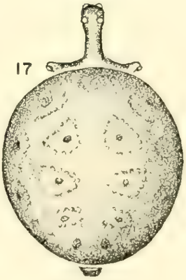
12


13


14


15


16


17


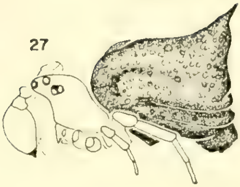
Figs. 18-20. *Phoroncidia scutula* (Nicolet), male. 18. Left palpus. 19. Lateral view. 20. Carapace and abdomen.

Figs. 21-23. *P. rubromaculata* (Keyserling), male. 21. Lateral view. 22. Sternum, coxae and abdomen, ventral view. 23. Carapace and abdomen, dorsal view.

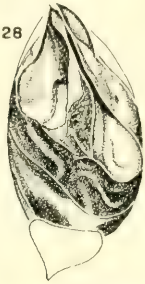
Figs. 24-26. *P. nicoleti* sp. n., male. 24. Palpus. 25. Lateral view. 26. Carapace and abdomen, dorsal view.

Figs. 27-29. *P. ravot* sp. n., male. 27. Lateral view. 28. Palpus. 29. Carapace and abdomen, dorsal view.

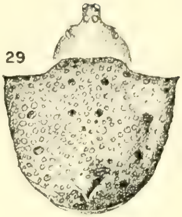
27



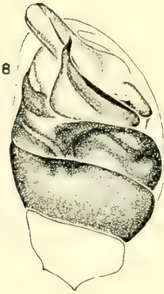
28



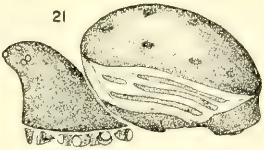
29



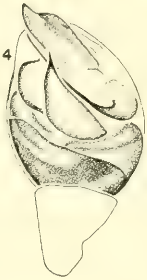
18



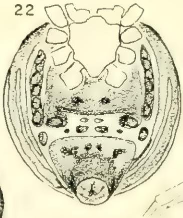
21



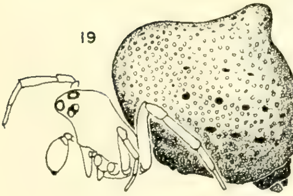
24



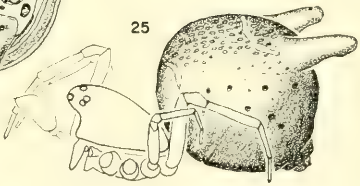
22



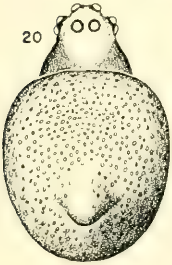
19



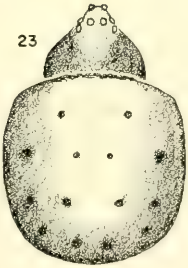
25

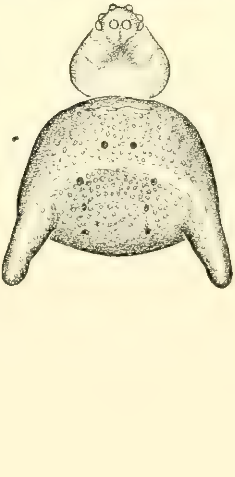


20



23



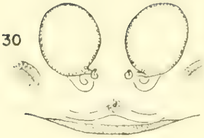


Figs 30-34. *Phoroncidia margamarga* sp. n., female. 30. Genitalia, dorsal view. 31. Epigynum. 32. Lateral view. 33. Sternum, coxae and abdomen, ventral view. 34. Dorsal view.

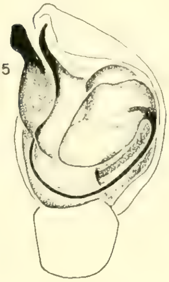
Figs. 35-37. *P. tina* sp. n., male. 35. Left palpus. 36. Lateral view. 37. Carapace and abdomen, dorsal view.

Figs. 38-41. *P. coquimbo* sp. n., female. 38. Genitalia, dorsal view. 39. Epigynum. 40. Lateral view. 41. Carapace and abdomen, dorsal view.

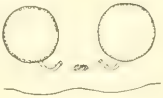
30



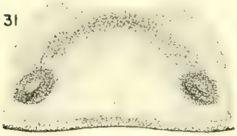
35



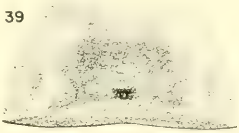
38



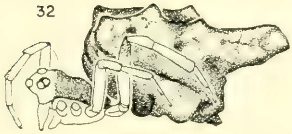
31



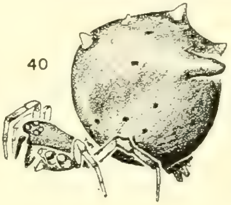
39



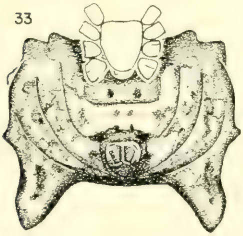
32



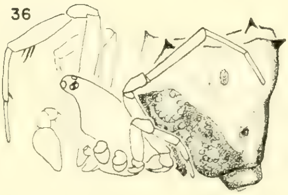
40



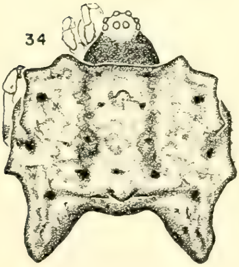
33



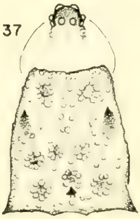
36



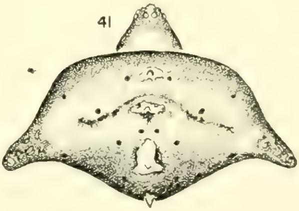
34



37



41

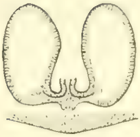


Figs. 42-45. *Phoroncidia scutellata* (Taczanowski), female. 42. Genitalia, dorsal view. 43. Epigynum. 44. Lateral view. 45. Dorsal view.

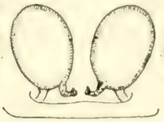
Figs. 46-51. *P. tricuspidata* (Blackwall), female, 46. Genitalia, dorsal view. 47. Epigynum. 48. Lateral view. 49. Abdomen, ventral view. 50, 51. Carapace and abdomen, dorsal view.

Figs. 52-56. *P. cribrata* (Simon), female. 52. Genitalia, dorsal view. 53. Epigynum. 54. Lateral view. 55. Sternum, coxae and abdomen, ventral view. 56. Carapace and abdomen, dorsal view.

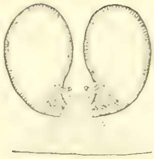
42



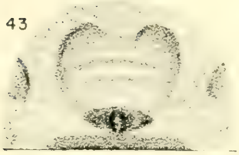
46



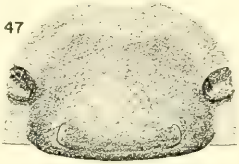
52



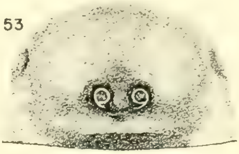
43



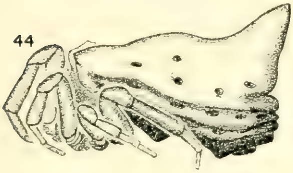
47



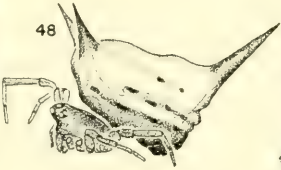
53



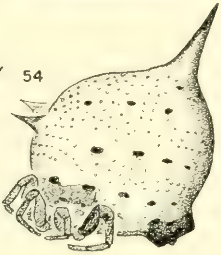
44



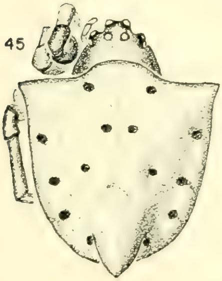
48



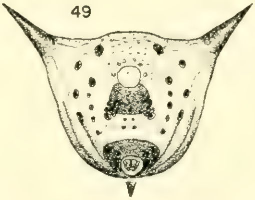
54



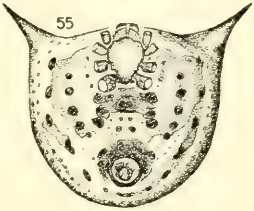
45



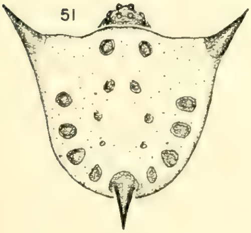
49



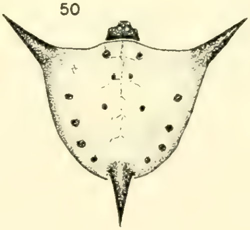
55



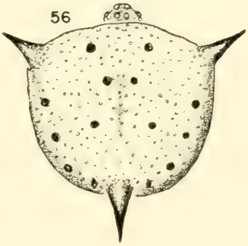
51



50



56

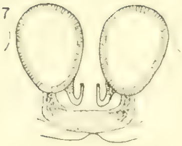


Figs. 57-61. *Phoroncidia flavolimbata* (Simon), female. 57. Genitalia, dorsal view. 58. Epigynum. 59. Lateral view. 60. Sternum, coxae and abdomen, ventral view. 61. Carapace and abdomen, dorsal view.

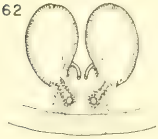
Figs. 62-65. *P. triunfo* sp. n., female. 62. Genitalia, dorsal view. 63. Epigynum. 64. Sternum, coxae and abdomen, ventral view. 65, 66. Carapace and abdomen, dorsal view. 65. Adult. 66. Juvenile.

Figs. 67-71. *P. biocellata* (Simon), female. 67. Genitalia, dorsal view. 68. Epigynum. 69. Lateral view. 70. Sternum, coxae and abdomen, ventral view. 71. Carapace and abdomen, dorsal view.

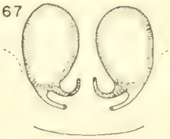
57



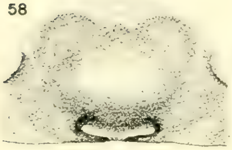
62



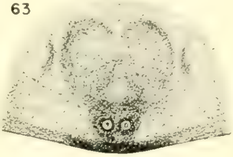
67



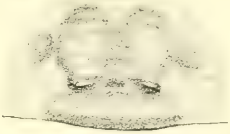
58



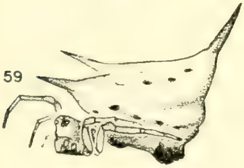
63



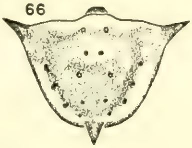
68



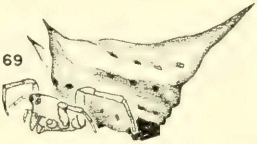
59



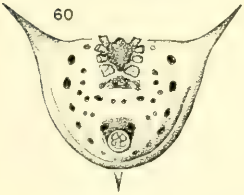
66



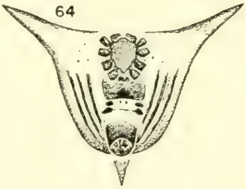
69



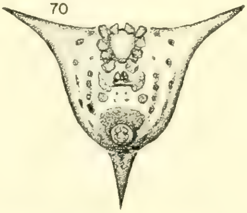
60



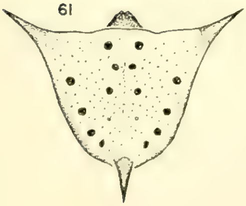
64



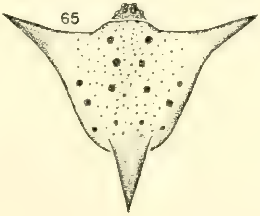
70



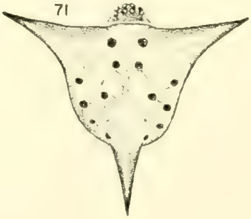
61



65



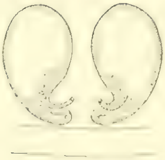
71

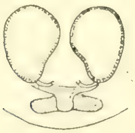


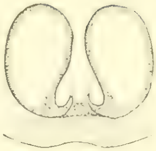
Figs. 72-76. *Phoroncidia saboya* sp. n., female. 72. Genitalia, dorsal view. 73. Epigynum. 74. Lateral view. 75. Abdomen, ventral view. 76. Carapace and abdomen, dorsal view.

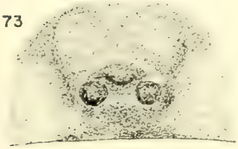
Figs. 77-81. *P. reimoseri* sp. n., female. 77. Genitalia, dorsal view. 78. Epigynum. 79. Lateral view. 80. Sternum, coxae and abdomen, ventral view. 81. Carapace and abdomen, dorsal view.

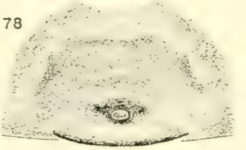
Figs. 82-86. *P. gira* sp. n., female. 82. Genitalia, dorsal view. 83. Epigynum. 84. Lateral view. 85. Sternum, coxae and abdomen, ventral view. 86. Carapace and abdomen, dorsal view.

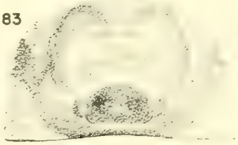
72


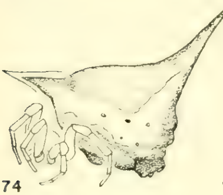
77


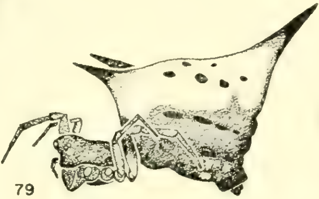
82


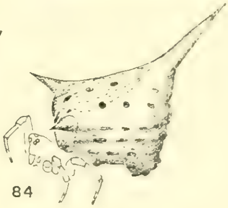
73


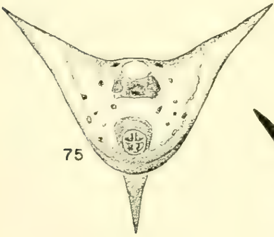
78


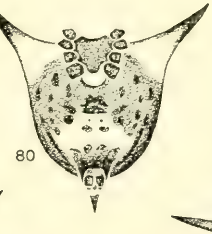
83


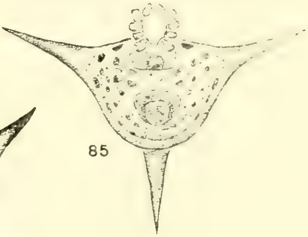
74


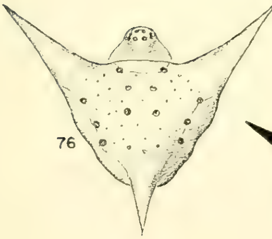
79


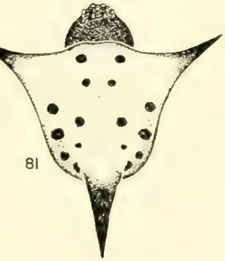
84


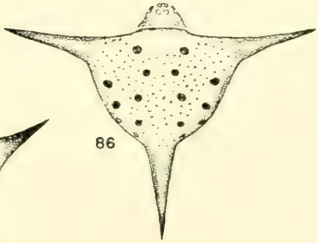
75


80


85


76


81


86


Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 4

THE BRAINCASE OF THE PALEOZOIC ELASMOBRANCH *TAMIOBATIS*

By Alfred Sherwood Romer

With One Plate

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
April 30, 1964

PUBLICATIONS ISSUED BY OR IN CONNECTION
WITH THE
MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

BULLETIN (octavo) 1863 — The current volume is Vol. 131.

BREVIORA (octavo) 1952 — No. 203 is current.

MEMOIRS (quarto) 1864–1938 — Publication terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 41 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 28 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained from the Publications Office of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Peters' Check-List of Birds of the World. Volumes 1, 4 and 6 are out of print; volumes 2, 3, 5, 7, 9, 10 and 15 are currently available.

Phylogeny and Evolution of Crustacea. Proceedings of a conference held at Cambridge, Mass., March 6-8, 1962. H. B. Whittington and W. D. I. Rolfe, editors. Cambridge, Mass., 192 pp., 80 figs., 1963. Cloth bound, $6.75.

Fishes of the Gulf of Maine, by Henry B. Bigelow and William C. Schroeder. Washington, viii - 577 pp., 1953. Photo-offset reprint, $6.50.

PUBLICATIONS OF THE
BOSTON SOCIETY OF NATURAL HISTORY

The remaining stock of the scientific periodicals of the Boston Society of Natural History has been transferred to the Museum of Comparative Zoology for distribution. Prices for individual numbers may be had upon request.

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 4

THE BRAINCASE OF THE PALEOZOIC ELASMOBRANCH *TAMIOBATIS*

By Alfred Sherwood Romer

With One Plate

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
April, 1964

Bull. Mus. Comp. Zool., Harvard Univ., **131**(4):87-105, April, 1964

No. 4 — *The Braincase of the Paleozoic Elasmobranch* Tamiobatis

By Alfred Sherwood Romer

INTRODUCTION

Eastman in 1897 described, as *Tamiobatis vetustus*, a specimen from Powell County, Kentucky, enclosed in a limestone nodule, which he believed to exhibit the dorsal surface of the braincase of a Devonian skate. However, the age of the specimen is uncertain; it is not a skate; it is the ventral, rather than the dorsal surface of the braincase that is exposed. In consequence, Eastman's structural identifications are quite erroneous. The *Tamiobatis* type is, nevertheless, of considerable importance, for it is the best preserved specimen of a Paleozoic elasmobranch braincase so far described. A few Paleozoic forms are represented by crushed slab materials in which little morphological detail can be made out. But of three-dimensional Paleozoic shark braincases, there have been described only two imperfect specimens. These are partial, late Devonian braincases, presumably of "*Cladodus*" type (Stensiö, 1937; Gross, 1937).[1]

Some years ago I was struck by the obvious resemblance of *Tamiobatis* to the pleuracanth braincases which I was then studying. The specimen (USNM No. 1717) was loaned to me through the courtesy of the Division of Vertebrate Paleontology of the United States National Museum. In earlier years complete development of the specimen would have been extremely difficult; thanks, however, to the newer methods of acid preparation developed at the British Museum by H. A. Toombs and A. E. Rixon, the limestone nodule has been completely etched away without harm to delicate surface structures of the braincase. Preparation was done with the aid of a National Science Foundation grant for study of Carboniferous vertebrates. I had originally planned to defer description of this specimen until after publication of work on the structure (internal as well as external) of the pleuracanth braincase. But since it currently appears that this study will not be completed for some time to come, I am publishing the present account, despite the fact that incomplete knowledge of the internal structure of older elasmobranch braincases may cause misinterpretation of the nature of foramina and other external features.

---

[1] A further Paleozoic shark braincase is currently being studied by Dr. D. H. Dunkle of the U. S. National Museum.

In the description below I have made no reference to Eastman's original description, since his belief that the originally exposed surface was dorsal rather than ventral invalidates his identifications. Thus, for example, the canals for the aortæ are identified by him as endolymphatic ducts, the pituitary fossa is said to be a dorsal fontanelle, the interorbital region is labelled rostrum, and the postorbital and otic processes are described as antorbital and postorbital processes, respectively.

Provenance of the Specimen

No data concerning the discovery of this specimen have been preserved in the records of the U. S. National Museum beyond the statement that it was found in the eastern part of Powell County, Kentucky. As may be seen from a geological map (Jillson, 1929), this small county includes strata ranging from Silurian at its western margin to lower Pennsylvanian (Pottsville) on the ridge-tops to the east. However, the stratigraphic possibilities can be readily narrowed down. On the one hand, the Pennsylvanian beds are continental shales and sandstones, and it is practically out of the question that a limestone nodule containing marine vertebrates could have been derived from them. On the other hand, Silurian and most Devonian beds are confined to the western part of the county, and the only Devonian strata reaching the eastern part of Powell County are the black shales of the late Devonian, in which (again) occurrence of a limestone nodule of this sort is most unlikely.

Considerable work in this general area is being done at the present time by the U. S. Geological Survey. It is the opinion of those familiar with the region that the specimen rather surely came from early Mississippian limestones present in eastern Powell County. Possibly a closer determination can be made when current studies of the region are completed.

DESCRIPTION

General. The general appearance of the braincase is readily seen in the illustrations. The surface of the cartilage was calcified to the extent of a millimeter or so. The calcified areas are dark in color; over a considerable area of the ventral surface, exposed before collection, the calcified material has been eroded, leaving a cast of the underlying region occupied by hyaline cartilage. Such areas are left white in the plate. The general proportions are obvious from either dorsal or ventral aspects, and such structural features as nasal processes, postorbital processes, the long otic region, with prominent lateral otic processes,

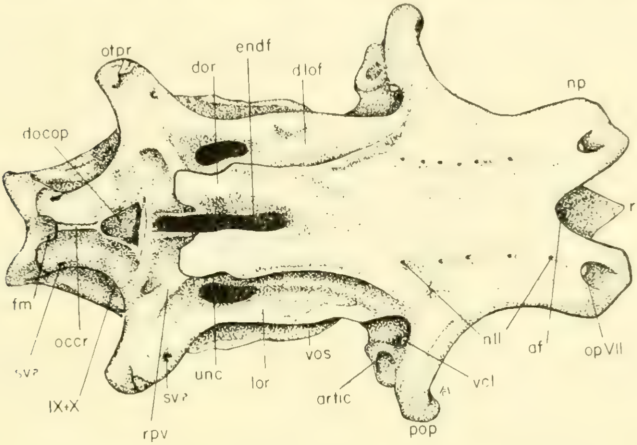


Fig. 1. Dorsal view of the braincase, slightly restored. × ½. Abbreviations for this and following figures: *af,* posterior border of anterior fontanelle; *artic,* articular facet for palatoquadrate; *cc,* point of entry of "common carotids" into braincase floor; *dlof,* dorsolateral otic fossa; *docop,* dorsal "opening" in occipital region; *dor,* dorsal otic ridge; *ec?,* impression of course of external carotid; *efh?,* foramen possibly for efferent hyoid artery; *endf,* endolymphatic fossa; *fm,* foramen magnum; *ic,* impressions of course of internal carotids toward pituitary region; *lor,* lateral otic ridge; *?mcv,* foramen probably for middle cephalic vein; *nll,* openings for supraorbital lateral line nerve twigs; *np,* nasal process; *occr,* occipital crest; *op V + VII,* foramen for ophthalmic rami of nerves V and VII; *op VII,* foramen for ophthalmic ramus of nerve VII; *os,* optic stalk; *otpr,* otic process; *pit,* pituitary region (eroded); *pop,* postorbital process; *pt VII,* canal for pretrematic ramus of nerve VII; *r,* calcified floor of base of rostrum; *rpv,* ridge covering posterior part of posterior vertical ear canal; *sos,* subocular shelf; *sv?,* foramina possibly for somatic nerve twigs; *unc,* uncalcified areas of braincase surface; *vcl,* foramen primarily for vena capitis lateralis; *vlof,* ventrolateral otic fossa; *vos,* ventral shelf in otic region containing passage for lateral head vein; *II,* optic foramen; *III,* oculomotor foramen; *IV,* trochlear foramen; $V_2 + V_3$, foramen for maxillary and mandibular rami of trigeminal nerve; V_3, groove for mandibular ramus of trigeminal; *VI?,* probable foramen for abducens nerve; *VII,* foramen for main trunk of facial nerve; *IX + X,* fossa for glossopharyngeal and vagus nerves.

and the occipital region, are apparent at first glance. A notable contrast with typical modern shark braincases is the long otic region. It seems quite certain that the braincase has undergone considerable dorsoventral crushing, so that the height (particularly in the otic region) is surely much less than was the case in life.

Nasal region. Anteriorly, as in modern sharks, the roof is deeply incised by the curved posterior margin of the anterior fontanelle, lying above the cavum precerebrale. Ventrally there is preserved, imperfectly, a thin sheet of calcified cartilage which represents a rostral structure. From its feeble nature it seems certain that the rostrum was short. On either side of the fontanelle the upper surface of the braincase extends anterolaterally to form a partial roof for the nasal region; a prominent foramen here is obviously for the emergence of the superficial ophthalmic ramus of nerve VII, innervating the lateral line organs of the snout.

Nasal capsules are not preserved and were presumably uncalcified. A nasal process is completely preserved on the right side; that of the left side is slightly imperfect anteriorly and laterally. From the tip of each process a narrow plate of calcified cartilage descends ventrally and posteromedially toward the floor of the braincase; this marks the anterior end of the plate of calcified cartilage which forms the inner wall of the orbital cavity and separates the orbit from intra-cranial areas. There is no foramen for an olfactory nerve in the anterior part of this plate, and hence this nerve lay medial to it and to the nasal process. The contours of the outer surface of this plate give no indication of the development of a nasal capsule lateral to it. It is hardly possible that the capsules could have been situated medially to these plates, filling — or nearly filling — the precerebral cavity. It seems reasonable to believe that these structures, not improbably essentially spherical in shape, projected forward, with the curved surfaces presented by the lateral edge of the rostrum and the plates descending from the nasal roof marking part of their ventral and lateral margins.

Orbital region. The braincase roof is very broad and nearly flat between the large orbits. On either side, the roof extends outward as a wide shelf, with a smoothly concave lateral outline, over the orbital cavities. A series of small foramina on either side allowed the passage of nerve twigs from the ophthalmic ramus of nerve VII to reach the neuromasts of the supraorbital lateral line canals.

Beneath this protecting roof, the upper part of the orbital wall shows a smooth sweep of its surface from the nasal region backward and, finally, outward to the anterior surface of the postorbital process. The superficial ophthalmic ramus of nerve VII obviously travelled forward well up beneath the roof (where are seen the inner openings of the small foramina for the supraorbital lateral line), to reach anteriorly the large foramen by which it gained the roof of the nasal region.

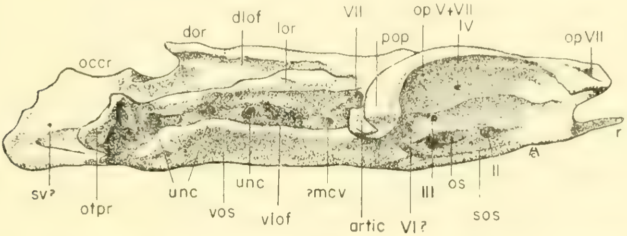


Fig. 2. Lateral view of the braincase, slightly restored. No attempt has been made to correct the marked dorsoventral crushing. Abbreviations as in Figure 1. × ½.

High up, posteriorly, is a large opening, directed anteriorly, which is surely for the exit of the ophthalmic rami of the trigeminal and facial nerves. Somewhat anterior and ventral to this is a small foramen in the appropriate position for emergence of the trochlear nerve and, farther ventrally, a somewhat larger foramen for the oculomotor nerve. Anteriorly, at about this vertical level, there develops a longitudinal ridge running forward toward the nasal region. Below this ridge there is present well anteriorly a large foramen, opening anterolaterally, which is presumably for the optic nerve. A narrow bar back of this foramen separates it from a long oval opening extending back much the length of the orbit not far above the floor. The upper and lower rims of this opening are somewhat everted; its posterior margin is curved strongly outward, and represents the anterior end of a swollen ridge which posteriorly subsides into the general contours of the cranial wall. The impression gained from this topography is that the opening provided for the emergence, anteriorly and laterally, of a cylindrical structure of some sort — obviously an eye stalk of typical elasmobranch type.

Openings for an ophthalmic (orbital) artery and a pituitary vein would be expected in the ventral part of the orbital cavity. I have been unable to make out such openings, presumably because of the crushing undergone here by the specimen.

Posterior to the position of the eye stalk, opposite the base of the postorbital process (and hence not seen in lateral view, but see Fig. 3A), there is a deep ventral recess, expanding anterolaterally from a large foramen. This was obviously for the emergence of V_2 and V_3 as well as, presumably, the lateralis nerves for the infraorbital and mandibular lateral line organs. Identification of a small imperfection in calcification as a foramen for nerve VI is less certain.

Ventrally, the orbital rim turns sharply outward to form a subocular shelf; this is far narrower than the dorsal rim. Anteriorly, the ventral surface of the braincase has been badly eroded, and it is possible that in life this shelf may have been more developed than the specimen now suggests.

Postorbital process. This process is highly developed. Its dorsal surface is convex in section, the anterior portion being a lateral continuation of the orbital roof. It curves markedly downward laterally. The anterior surface, conforming to the spherical contour of the orbit, is essentially a smooth wall, vertical below, curving outward above (Fig. 3A). From the ventral base of the anterior surface of the process a distinct groove, bounded below by the subocular shelf, extends outward for some distance. This may have served as a channel for the mandibular ramus of the trigeminal nerve. Distally, the postorbital process proper curves forward as well as downward. Back of this area

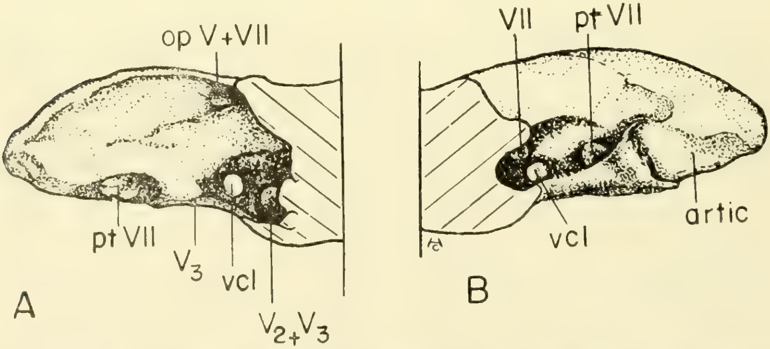


Fig. 3. *A*, anterior, and *B*, posterior views of the right postorbital process. Abbreviations as in Figure 1. × ½.

(Fig. 3B) is a well-defined articular surface, concave in cross section, for the palatoquadrate. Its curved anterodorsal boundary is the posterior border of the postorbital process proper, its ventrolateral boundary a ridge situated on a posterior accessory buttress of the postorbital process. Posteriorly, proximal to the articular area, the postorbital process is pierced diagonally by a prominent foramen. Its median opening enters the process well ventrally on the posterior surface; it emerges on the anterior surface just above a lateral extension of the subocular shelf. This foramen may have served for the passage forward of the pretrematic ramus of the facial nerve. At the base of the process a large foramen, surely carrying the vena capitis lateralis, pierces it in an anteroposterior direction. This leads from the ventral part of the orbital area, dorsolateral to the foramen for V_2-V_3, back to a ventrolateral shelf area in the otic region.

Otic region. As noted above, the otic region is very long, as compared with that of modern elasmobranchs. Even excluding the occipital region from comparison, the length here is much in excess of the anterior portion of the braincase. It is broad as well as long (although the seeming relative breadth is undoubtedly exaggerated because of dorsoventral crushing). For much of its length the median roof area is slightly concave in section — this a continuation of a slight median depression present in the interorbital region. Medially in the posterior half of the roof is an elongate fossa which obviously included the openings of the endolymphatic ducts. Posteriorly, this opening is surrounded by a low raised ridge; for most of its length, however, it is bordered by a pair of prominent ridges, which may be termed the dorsal otic ridges. For the anterior two-thirds of their lengths these ridges have laterally a sharp curved border, somewhat concave in outline in dorsal view. This may have lain parallel to the upper inner margin of the palatoquadrate, with which it may have had a ligamentous connection. Posteriorly, the processes become narrow, and are mildly swollen on their dorsal surfaces. Distally, their terminations overhang somewhat flattened areas on either side of the posterior end of the endolymphatic fossa; these areas were presumably occupied by median dorsal segments of the axial musculature, and the tips of the processes may have been in continuity with some type of "nuchal" ligaments. As shown by sections of pleuracanth braincases (similarly built in this region), the anterior vertical canals of the internal ear lay beneath the anterior portions of the dorsal otic ridges, and part of the posterior vertical canals lay beneath the posterior portion of the ridges.

Projecting laterally, the length of the otic segment, is a longitudinal ridge, rounded in section, which may be termed the lateral otic ridge. As shown by pleuracanth specimens, this lateral ridge contained the horizontal canal of the internal ear — a canal of remarkable length. Between dorsal and lateral otic ridges is a deep longitudinal hollow, which may be termed the dorsolateral otic fossa. The posterior boundary of the fossa is a low rounded ridge which descends posterolaterally from the dorsal otic ridge; this presumably overlies the posterior end of the posterior vertical canal. In the floor of the fossa is an oval area, broader posteriorly, in which no calcification of cartilage is present. I believe that this represents merely an absence of calcification in the surface cartilage in this region; it is improbable that any opening was present here in life. No further openings are apparent in the boundaries of the dorsolateral otic fossa. It may have been partially occupied by axial musculature.

Below the lateral otic ridge is a second longitudinal channel, which we may term the ventrolateral otic fossa. Its dorsal border is the lateral otic ridge; its floor a lateral extension of the basicranial floor, which curves upward as well as outward. This upward curvature results in the formation of a longitudinal trough which extends most of the length of the fossa; its outer margin is somewhat concave in contour as seen from above or below, although with a slight lateral projection (possibly post-mortem) at mid-length. Posteriorly this trough, which obviously carried the vena capitis lateralis, opens laterally somewhat short of the end of the otic region. Above the level of the trough and just behind the postorbital process a well-developed foramen opens outward and backward. This is undoubtedly the opening for the facial nerve. An opening posteroventral to this is perhaps for a middle cephalic vein. Farther posteriorly there are, on both sides of the specimen, two oval uncalcified areas on the inner wall of the fossa. I cannot interpret them as being to any degree functional; they are too far anterior for either to be reasonably interpreted as for nerve IX.

Posteriorly, on either side, the otic region expands laterally into a prominent lateral otic process. The dorsal surface of the process is for the most part gently convex; its proximal part was presumably underlain by the posterior end of the horizontal semicircular canal. Close to its anterior end is a tiny dorsal foramen which may have carried some component — ?somatic — of the IX-X nerve complex. The distal end of the process and the distal part of its anterior margin terminate in thin blunt ridges which would appear to have been articular in nature, perhaps having contact with some anterior member or members of the gill arch series of cartilages. The anterodistal terminus of the process is tilted prominently upward.

A very considerable part of the anterior face of the lateral otic process is lacking in calcification; this area is quite irregular in outline, as may be seen in the figures. But no reason can be adduced for such a prominent lack of chondrification. It is improbable that the condition seen in the specimen was due to post-mortem loss of surface, for this region was not exposed to weathering of the nodule, and despite the irregularity of the "opening" here, closely similar patterns are present on both sides.

As noted below, the under side of the otic process is deeply undermined posteriorly. On either side, the calcified base of the otic process is separated from the basal plate of the braincase by a narrow slit in which no calcification is present. Whether this slit existed in life, and represents a persistent marker between otic and occipital cartilages, or whether this is due to post-mortem crushing, is uncertain.

Occipital region. This is relatively short, constricted in width posteriorly, and of lesser depth than the otic region. Dorsally, indications of division betwen otic and occipital regions are seen in the form of slight ridges which begin, on either side, lateral to the posterior end of the endolymphatic fossa and curve outward and backward to the posterior margin of the base of the otic processes. Certain of the markings here are apparently post-mortem in nature, but probably represent, in any event, indications of structural weakness at the points of fusion of elements embryologically discrete. (No indications of separation of units are visible ventrally.)

Just posterior to a low transverse ridge behind the endolymphatic fossa is a large triangular opening, facing dorsally. At first glance one would assume, from its position, that this is the foramen magnum. This, however, is not the case, but the nature of this opening is unknown. Possibly it merely represents an uncalcified area in the braincase roof, but against this interpretation is the fact that the opening shows a distinct, if low, boundary ridge. Posterior to this opening there is a median occipital crest (incompletely preserved in the specimen). Below the posterior termination of this ridge lies the foramen magnum; this is nearly completely obscured by dorsoventral crushing. The dorsal portion of the occipital segment is relatively narrow, its lateral boundaries curving medially and posteriorly from the posterior margin of the otic processes. This dorsal area, bounding laterally the triangular dorsal opening, described above, and the occipital crest, is gently convex in vertical section; there is present here a small foramen, perhaps for a "spino-occipital" somatic nerve ramus.

Farther ventrally the occipital segment is much broader than it is dorsally, its lateral margins curving inward and then backward, from a point well out beneath the otic processes. The upper surface of this thin ventral region forms the floor of a cavity of considerable size which extends forward, contracting in width in its course, beneath the main expansion of the otic process and the dorsolateral margins of the occipital segment. This cavity was not explored to its full depth, but surely formed the exit for the vagus nerve and not improbably the glossopharyngeal as well. I believe I can make out, in the lateral wall of the cavity near its posterior end, the inner opening of the small foramen in the otic process, mentioned above, which may have carried a small somatic branch of the glossopharyngeal or vagus.

The occipital condyle is, as preserved, much broader than high; it is V-shaped in contour as seen from above or below, and deeply indented centrally, presumably for the notochord.

Ventral surface. The ventral surface of the specimen was exposed when found and had been subject to weathering. The light-colored areas shown in the plate are regions in which weathering had removed the thin surface calcification of the braincase floor; except anteriorly the damage was not severe. The ventral surface was essentially flat. In the interorbital region the lateral margins follow the curved line of the shelf underlying the orbit which, as noted earlier, has been destroyed in part by erosion. Behind the postorbital processes the floor broadens greatly, its lateral borders curving upward somewhat to form the margins of the trough which carried the vena capitis lateralis. Beyond the otic process there is a moderate constriction in width to the margins of the condyle. As suggested by the pattern of erosion, there were slight longitudinal ridges on either side of the midline toward the back; these merged anteriorly.

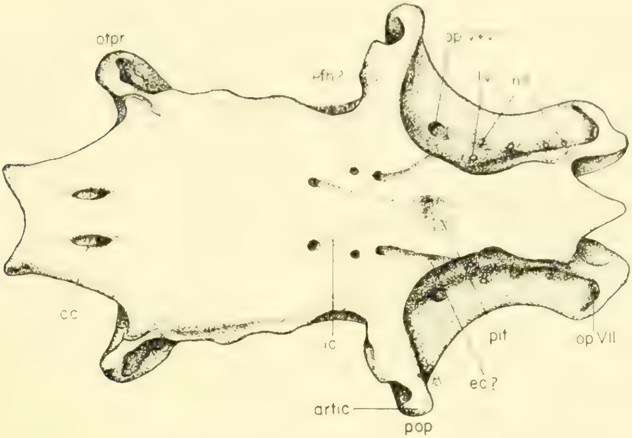


Fig. 4. Ventral view of the braincase; the pituitary region is imperfectly preserved. Abbreviations as in Figure 1. × 1½.

Posteriorly the braincase extends to a greater depth than in typical modern elasmobranchs, for the paired anterior continuations of the dorsal aorta ("common carotids") entered the braincase floor a short distance anterior to the condyle. Well forward in the otic region a pair of openings presumably mark the exit of the carotids from the aortic canals, and, as may be seen from the plate, there is evidence of grooves — presumably for internal carotids — leading from these foramina forward and medially toward the hypophysial region. Farther forward on each side is a foramen which may have been the point of entrance of the hyomandibular (pseudobranchial) artery. Still farther forward on either side is a further opening, from which a deep groove leads forward and outward into the orbit; presumably this was for an external carotid.

It is unfortunate that almost the entire surface layer of calcified cartilage has been lost in the hypophysial region; however, it is reasonable to believe that the surface of the matrix essentially follows the surface contours. There was here a large oval depression, which may have contained an open hypophysial pit. Paired indentations leading forward from the front end of this depression suggest that the two internal carotids entered the braincase independently here.

COMPARISONS

As noted above, uncrushed Paleozoic elasmobranch braincase material exists otherwise only in the case of the two late Devonian specimens of "*Cladodus*" and the pleuracanth material from the Permian which I am currently studying. The *Tamiobatis* type may be compared with these forms.

The specimen studied by Stensiö (1937) and named *Cladodus hassiacus* by Gross (1937) includes only the ventral half of the middle portion of the braincase. The roof is nowhere present; the specimen ends anteriorly without including the front borders of the orbit and terminates posteriorly part way along the otic region. As far as preserved, the general proportions are comparable to those seen in *Tamiobatis*. The optic nerve, eye stalk, main trigeminal opening, and more dorsal opening for ophthalmic rami are present as in *Tamiobatis*, but the last two foramina are apparently less developed than in our type. Due to crushing and erosion, I cannot tell whether or not *Tamiobatis* had a notch for palatoquadrate articulation (*obf* in Stensiö's figure 1) or whether the ventral bloodvessel openings which he figures were present. Stensiö has restored the nasal region directly from *Chlamydoselachus*, but there is no specific reason for assuming that the pattern was of the fashion found in that modern genus. Of the postorbital process only the lower portion was present in his specimen, and, probably as a consequence, it appears to be slimmer than in *Tamiobatis*. Quite surely, had the process been better preserved, there would have been found, as in *Tamiobatis* and in Gross' specimen, an articular facet for the palatoquadrate, and not improbably a canal of the sort which I have suggested as carrying the pretrematic ramus of the facial nerve (perhaps the notch which he illustrates at the tip of his postorbital process represents the remains of this canal). Stensiö in his figure 3 shows, on the left side, two canals emerging posteriorly from the base of the postorbital process, of which the upper is labelled as for the jugular vein, the lower for the main trunk of the facial nerve. The course indicated for the jugular is in an unusually high position for that vein, and I suggest that with better material it would be found that (as in *Tamiobatis*) it is the ventral canal which carries the lateral head vein and that the dorsal opening is that for the facial nerve.

As indicated by his figure 5 and the text, the canal region of the ear was incompletely preserved in Stensiö's specimen. Apparently parts, at least, of all three canals were present in his specimen. However, they appear to occupy a short space anteroposteriorly — much shorter than is the case in pleuracanths, *Tamiobatis*, or (apparently) in Gross' specimen of "*Cladodus.*" This seeming abbreviation may well be due to crushing and imperfections at the posterior end of Stensiö's specimen.

In Stensiö's, as in Gross' specimen, in *Tamiobatis* and in pleuracanths, and in contrast with Recent elasmobranchs, the "common carotids" are carried well forward ventrally in the base of the braincase. A series of foramina farther forward in the braincase floor agree well in general with those described by Gross and those present (in incomplete fashion) in *Tamiobatis*.

Stensiö's specimen is incomplete posteriorly; he arbitrarily terminates the braincase in his figure 6 at a distance from the orbit comparable to that seen in modern elasmobranchs. Due to this arbitrary posterior termination, and to his restoration of the nasal region in accordance with that of *Chlamydoselachus*, the general picture of the braincase in his figure 6 is very similar to that of modern sharks. But quite surely better preservation of the specimen would have shown very different proportions, much more in keeping with Gross' *Cladodus wildungensis*, *Tamiobatis* and pleuracanths. In this instance, as in the further specimens to be discussed, certain features (the presence of an optic stalk, etc.) are closely comparable to those in modern elasmobranchs; others (as the canals for the "common carotids") are features probably of a primitive nature, lost or modified in modernized forms.

The specimen studied by Gross (1937) and referred to *Cladodus wildungensis* is from the same horizon and locality (Wildungen) as that of Stensiö, and considered by him to be generically identical. It is much more complete. Anteriorly, it includes the posterior margins of the dorsal fontanelle, and thus lacks only a small area of presumed calcification in the nasal region; posteriorly much of the endolymphatic slit is present. and hence there has been lost only the short occipital region and the posterior end of the otic region (with the otic processes). The specimen is somewhat larger than *Tamiobatis*, but resembles that type closely in general proportions in both dorsal and ventral views, and has the great advantage of being uncrushed. Whereas, for example, this *Cladodus* specimen is but 20 per cent or so larger than *Tamiobatis* in dimensions measured on both upper and lower surfaces, its height at (for example) the level of the postorbital processes is approximately double that of the *Tamiobatis* type.

As may be seen by comparing Gross' figure 1 with Figure 1 of this paper, his braincase is in dorsal view very similar to that of *Tamiobatis*. Both show the notch for an anterior fontanelle, a broad interorbital region forming laterally a roof for the large orbit, and a row of nerve foramina for the supraorbital lateral line canal. In both there is a prominent postorbital process (somewhat imperfect dorsodistally in the Gross specimen). In this specimen we find definite proof that — in contrast to Stensiö's assumption — there was a greatly elongated otic region. As in *Tamiobatis*, there is a well-marked area of the dorsal ridges such as I believe were apposed to the palatoquadrates. Centrally and posteriorly there is an elongate endolymphatic opening like that of *Tamiobatis*. As in that form, a swelling (*hB*) posterolateral to that opening is obviously related to the posterior vertical canal, thus showing that in "*Cladodus*," contrary to Stensiö's interpretation of a much poorer specimen, the canal region was greatly elongate. Dorsally, Gross' specimen becomes imperfect posteriorly before the end of the endolymphatic slit is reached. He tends to assume (presumably influenced by a comparison with modern sharks) that the terminus of the roof of the braincase had been nearly attained at this point. But comparison with *Tamiobatis* strongly suggests that a considerable area is absent here, including projecting otic processes. It is unfortunate that it cannot be said whether the dorsal ridges terminated in the prominent posteriorly-projecting processes seen in *Tamiobatis* and pleuracanths.

Ventrally, Gross' specimen again compares closely with *Tamiobatis;* his figure 5 (except for the absent otic processes) compares closely with my Figure 4.

The structure of the orbital region, seen in Gross' figures 3A and 3B, is comparable in most respects to Stensiö's findings and those seen in *Tamiobatis* (Fig. 2). In all three there is a prominent oval for an eye stalk, an optic nerve foramen anterior to it, and more dorsally, foramina for nerves III and IV. As in the case of Stensiö's specimen, Gross was able to make out ventral foramina for an ophthalmic artery and pituitary vein — structures which crushing appears to have obliterated in *Tamiobatis*. In *Tamiobatis* there appears to be a single opening in the posterodorsal corner of the orbit for ophthalmic rami; in *C. wildungensis* there are two distinct openings here (*O Sup*, *O Sup?*). I am unable to completely reconcile the foramina for various elements of V and VII as determined by Gross with those which I appear to find in *Tamiobatis* or those identified by Stensiö. As in *Tamiobatis*, but in disagreement with Stensiö's description of his specimen, there is but a single anteroposterior canal traversing the base of the postorbital process. As noted above, the postorbital process was incompletely preserved in *C. hassiacus;* that in *C. wildungensis* agrees well with that of *Tamiobatis* in the presence of a canal for the pretrematic ramus of the facialis and a distinct articular area for the palatoquadrate.

In sum, apart from a few differences regarding nerve foramina, possibly due to imperfections in the materials, the braincase described by Gross agrees in almost every preserved feature with *Tamiobatis*. It is obvious, assuming that *Cladodus wildungensis* and *Cladodus hassiacus* are really related, that the proportions attributed by Stensiö to the braincase in his specimen are (literally) far short of the truth as regards its length.

As noted earlier, I have long had in my possession considerable materials of "*Pleuracanthus*" from the Lower Permian of Texas, and had, a number of years ago, begun a study of the braincase, including the serial sectioning of a number of specimens. I hope to complete this study in the not distant future, and will postpone any detailed comparison of this material with *Tamiobatis* and "*Cladodus*" until this has been done. It may be said in the meantime, however, that as far as can be seen at present, agreement is very close. If such a figure as that of the dorsal surface of the pleuracanth skull published by me in 1933 (fig. 26; 1945, fig. 55)[1] be compared with that of *Tamiobatis*, it will be seen that the two are similar in all general regards (except for a somewhat greater lateral projection of the otic processes in *Tamiobatis*), and the same holds true for many other features of the anatomy.

CONCLUSION

I had at one time thought that, due to the great similarity between the pleuracanths and *Tamiobatis*, the latter might be an early representative of the pleuracanth group. Against this is the fact that pleuracanths are mainly freshwater forms, whereas *Tamiobatis* is from a marine limestone. This is not a crucial argument, for the later pleuracanths may well have migrated from salt water to fresh, and *Tamiobatis* might have been an ancestral marine form. But since the "*Cladodus*" specimens are, as far as known, in essential agreement with *Tamiobatis* and the pleuracanths, it is more reasonable to believe that we are here dealing with a truly primitive elasmobranch type of braincase, characteristic of ancestral shark types in the Devonian, not improbably retained in more generalized Carboniferous forms, and persistently retained by the pleuracanth side-branch of the shark group.

---

[1] Hussakof's figures of this skull type (1911, pl. 29) are grossly inaccurate, in a fashion similar to Eastman's misinterpretation of *Tamiobatis*, with dorsal and ventral surfaces reversed, the postorbital process identified as nasal capsule, etc.

The most conspicuous difference between this type of primitive shark braincase and that of modern genera is, of course, the very long otic and occipital segments of the primitive braincase, with the more "expansive" development of the braincase cartilages to include the anterior part of the dorsal aorta within its substance. So radical are the differences in proportion here that it was not surprising that, in default of more complete material, Stensiö restored his *Cladodus* specimen in abbreviate modern fashion. I regard it as highly probable that all later elasmobranchs are descended from Triassic hybodonts; in these forms shortening of the otic region had already occurred (cf. *Hybodus*, as figured by Smith Woodward, 1916, fig. 3). It is to be hoped that further discoveries of Paleozoic sharks may at some future time give us knowledge of the phylogenetic point at which this shortening occurred, and of the associated functional "reasons" (no doubt complex). It is of interest, in view of the belief of many that the elasmobranchs are allied to the placoderms, that in many members of that important Devonian group the "facial" region was, as in the older sharks, relatively short, and the otic plus occipital regions often greatly elongated. The change in proportions seen in the evolutionary history of the elasmobranch "skull" may well be merely one of a number of parallel developments in this regard in higher fishes and lower tetrapods. For example, the long-standing confusion as to the nomenclature of the dermal roofing elements of the frontal-parietal regions in rhipidistians was due to the fact that in the evolutionary series rhipidistians – amphibians – reptiles there was a long-continued trend toward relative reduction of the otico-occipital region, with a concomitant rearrangement of the overlying dermal elements (Westoll, 1938; see Romer, 1941, fig. 4).

One thus gains the impression that there has been, in the history of the gnathostome fishes, a strong trend toward relative reduction of the posterior portion of the cranial structures and, very probably, a concomitant elaboration of the "facial" region. Study of the functional changes which underlie this trend may be worthy of pursuit.

REFERENCES

EASTMAN, C. R.

1897. *Tamiobatis vetustus;* a new form of fossil skate. Amer. Jour. Sci., (4) **4**: 85-90.

GROSS, W.

1937. Das Kopfskelett von *Cladodus wildungensis* Jaekel. 1. Teil. Endocranium und Palatoquadratum. Senckenbergiana, **19**: 80-107.

HUSSAKOF, L.

1911. The Permian fishes of North America. Carnegie Inst. Washington, publ. **146**: 155-175.

JILLSON, W. R.

1929. Geologic map of Kentucky. Kentucky Geological Survey, Frankfort, Ky.

ROMER, A. S.

1933. Vertebrate paleontology. Chicago, 491 pp. 2nd ed., 1945, 687 pp.

1941. Notes on the crossopterygian hyomandibular and braincase. Jour. Morph., **69**: 141-160.

STENSIÖ, E. A.

1937. Notes on the endocranium of a Devonian *Cladodus*. Bull. Geol. Inst. Upsala, **27**: 128-144.

1945. On the heads of certain arthrodires. Kungl. Svenska Vetensk. Handlingar, (3) **22** no. 1: 1-70.

WESTOLL, T. S.

1938. Ancestry of the tetrapods. Nature, **141**: 127-128.

WOODWARD, A. S.

1916. The fossil fishes of the English Wealden and Purbeck formations. Palaeontographical Society, London, volume for 1915: 1-48, pls. I-IX.

(Received August 26, 1963)

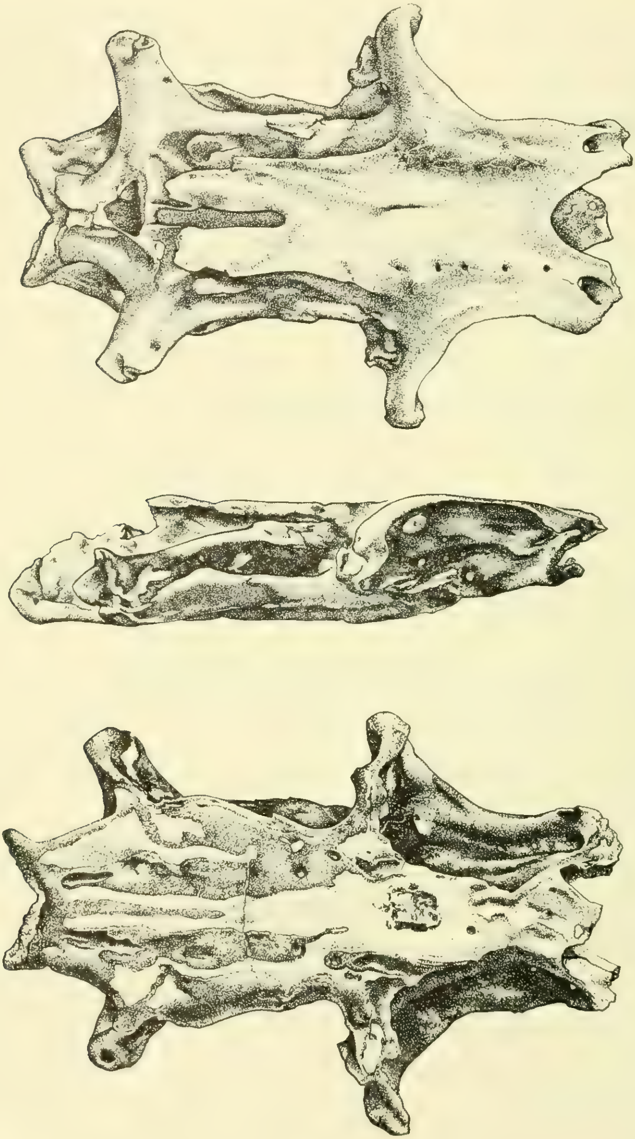


Plate 1.

Dorsal, lateral and ventral views of the type braincase of *Tamiobatis vetustus*, as preserved. The height has obviously been reduced by crushing. White areas on the ventral surface are those in which superficial calcification has been removed by erosion. × ½. Drawn by N. Strekalovsky.

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 5

THE TAXONOMIC STATUS OF *HEPTAXODON* AND DENTAL ONTOGENY IN *ELASMODONTOMYS* AND *AMBLYRHIZA* (RODENTIA: CAVIOMORPHIA)

By

Clayton E. Ray
United States National Museum

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
May 25, 1964

PUBLICATIONS ISSUED BY OR IN CONNECTION WITH THE

MUSEUM OF COMPARATIVE ZOOLOGY

HARVARD UNIVERSITY

BULLETIN (octavo) 1863 — The current volume is Vol. 131.

BREVIORA (octavo) 1952 — No. 204 is current.

MEMOIRS (quarto) 1864–1938 — Publication terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 41 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 28 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained from the Publications Office of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Peters' Check-List of Birds of the World. Volumes 1, 4 and 6 are out of print; volumes 2, 3, 5, 7, 9, 10 and 15 are currently available.

Phylogeny and Evolution of Crustacea. Proceedings of a conference held at Cambridge, Mass., March 6-8, 1962. H. B. Whittington and W. D. I. Rolfe, editors. Cambridge, Mass., 192 pp., 80 figs., 1963. Cloth bound, $6.75.

Fishes of the Gulf of Maine, by Henry B. Bigelow and William C. Schroeder. Washington, viii - 577 pp., 1953. Photo-offset reprint, $6.50.

PUBLICATIONS OF THE BOSTON SOCIETY OF NATURAL HISTORY

The remaining stock of the scientific periodicals of the Boston Society of Natural History has been transferred to the Museum of Comparative Zoology for distribution. Prices for individual numbers may be had upon request.

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 5

THE TAXONOMIC STATUS OF *HEPTAXODON* AND DENTAL ONTOGENY IN *ELASMODONTOMYS* AND *AMBLYRHIZA* (RODENTIA: CAVIOMORPHA)

By

Clayton E. Ray
United States National Museum

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
May, 1964

Bull. Mus. Comp. Zool., Harvard Univ., 131(5): 107-127, May, 1964.

No. 5 — *The Taxonomic Status of* Heptaxodon *and Dental Ontogeny in* Elasmodontomys *and* Amblyrhiza (*Rodentia: Caviomorpha*)

By

CLAYTON E. RAY[1]
United States National Museum

INTRODUCTION

The affinities of the extinct Puerto Rican caviomorph, *Heptaxodon bidens* Anthony 1917, have been problematical owing to the supposed reduction of cheek teeth to two on either side above and below, with the first strongly dominant. This condition, grossly aberrant for a caviomorph, led some authors to isolate *Heptaxodon* in its own monotypic family (Miller and Gidley, 1918, p. 447, followed by Anthony, 1926, p. 130) or subfamily (Anthony, 1917, p. 186; 1918, p. 397). Others have included it in a subfamily (Simpson, 1945, p. 96, followed by Wood, 1955, p. 182) or family (Landry, 1957, p. 59) together with five[2] other West Indian genera. If the stated diagnostic characters of *Heptaxodon* are accepted at face value, association at the familial level with any known genus of caviomorph seems indefensible. The down-grading in taxonomic isolation of *Heptaxodon* in the more recent works cited above undoubtedly reflects a growing disbelief in the reality of its apparent uniqueness, but it was H. G. Stehlin (*in* Stehlin and Schaub, 1951, p. 262, followed by Schaub, 1958, p. 736) who first interpreted the genus as a growth stage of *Elasmodontomys obliquus* Anthony 1916. This author arrived at the correct conclusion on the invalid premise that the dominant cheek teeth of *Heptaxodon* are P$\frac{4}{4}$ of *Elasmodontomys*. X-ray photographs of critical specimens, restudy of all dentigerous elements of *Heptaxodon*, *Elasmodontomys*, and *Amblyrhiza* in the collections of the American Museum of Natural History (AMNH) and the Museum of Comparative Zoology (MCZ), and comparisons with developmental patterns in hystricomorphs and in other caviomorphs have shown, as pointed out in detail below, that the anterior cheek teeth of *Heptaxodon* are DP$\frac{4}{4}$ of *Elasmodontomys*. This review of the evidence has made possible a better understanding of dental ontogeny in *Elasmodontomys* and *Amblyrhiza*.

---

[1] This work was completed while the author was Assistant Curator in charge of fossil vertebrates at the Florida State Museum, University of Florida, Gainesville.

[2] Six, if *Quemisia*, omitted by the above authors, were included in the group, as it has been to the present by all authors who have discussed it.

A word is necessary here regarding nomenclature of tooth components. Stirton (1935, p. 392) has derived from the tritubercular system a terminology for beaver teeth, and Fields (1957, p. 278) has extended it with additions to certain late Miocene dinomyids, pointing out that "the application of these terms does not necessarily imply homology but has been used as a matter of convenience." I have not felt justified in extending to the highly evolved, hypsodont *Elasmodontomys* a system which ordinarily carries some connotation of homology. Further, the structure of the *Elasmodontomys* cheek tooth is so elegantly simple that it is most conveniently described in neutral geometric and numerical terms.

Cope (1883, p. 5) has aptly characterized the units of which the cheek tooth of *Amblyrhiza* is composed as "columns of dentine inclosed in . . . a sheath of enamel," a description equally appropriate for *Elasmodontomys.* The columns and their sheaths are flattened anteroposteriorly and closely applied to one another, with a small amount of cementum interspersed. Successive columns are separated by transverse reëntrants that penetrate the full width of the tooth. Each reëntrant may be designated as outer or inner depending on whether its deepest proximal extension is labial or lingual. Individual columns and reëntrants may be distinguished by numbering them serially from anterior to posterior in each tooth. The enamel of the anterior wall of each column (and thus the posterior wall of each reëntrant) is much thicker than that of the posterior wall (anterior wall of reëntrant) in the upper teeth, and vice versa in the lower teeth. In both upper and lower teeth the free external enamel walls are invariably thick. Much confusion has arisen in describing these teeth as a result of inconsistent reference to either columns or reëntrants, and as a result of failure to detect the thin enamel walls, which appear only as hairlines on occlusal surfaces. The occlusal pattern of each column obliquely sectioned by wear takes the form of a much flattened ellipse. In some cases, even in long, little-worn teeth some reëntrants are not completely penetrant but have their vertex tightly appressed to the adjacent external enamel wall so that it is visible far down the shaft of the tooth through the translucent external wall. In such cases, and in senescent teeth in which the enamel forms a single continuous trace on the occlusal surface, the pattern produced by each column is more appropriately designated a loop.

Development of the lower dentition of *Elasmodontomys* will be treated first, followed by the less well documented upper dentition of *Elasmodontomys*, and that in turn by the fragmentary data on *Amblyrhiza*. Length of a given tooth is in all cases a maximum taken parallel to the longitudinal axis of the tooth, including roots where present. Selection of genera for comparison has been in part dictated by the availability of appropriate ontogenetic stages, and no *a priori* implication of relationship is intended.

I wish to thank Professor Bryan Patterson, who initiated the present study, for generously turning over to me X-rays prepared by Dr. Rainer Zangerl of the Chicago Natural History Museum (CNHM) together with the drawings by Mrs. Dorothy Marsh that are reproduced in Figures 1 and 2. I wish to thank also the curators in the Department of Vertebrate Paleontology, American Museum of Natural History (AMNH), who permitted free use of the splendid collection of Antillean caviomorphs accumulated largely by H. E. Anthony; and the curatorial staffs of the mammal departments of the American Museum of Natural History, Chicago Natural History Museum, and Museum of Comparative Zoology (MCZ) for making available modern comparative material.

DENTAL ONTOGENY

Lower Dentition of *Elasmodontomys*

Certain critical specimens are described below in detail in order of increasing age, followed by a discussion of development and comparisons with other genera. AMNH 55030 and 55031, and MCZ 10132 have always been regarded as "*Heptaxodon*," whereas AMNH 55037, in spite of its DP_4, was identified quite correctly as *Elasmodontomys*.

AMNH 55030. Left ramus with DP_4 (Fig. 1A). Figured by Anthony (1917, pl. 5, figs. 4, 6; 1918, fig. 38C, D, F; 1926, fig. 48C, D, F). Mandibular symphysis open. Bone porous in texture. DP_4 with five columns, the first with a small, semi-isolated subsidiary pillar on its anterolingual wall, the pillar unworn, merging with the column at the alveolar border; the fourth column with a constriction in the middle of its occlusal surface. Occlusal area small; obviously it would have increased with additional wear. The X-ray photograph shows incipient double roots of DP_4 (reflected externally by a bulge on the ventral

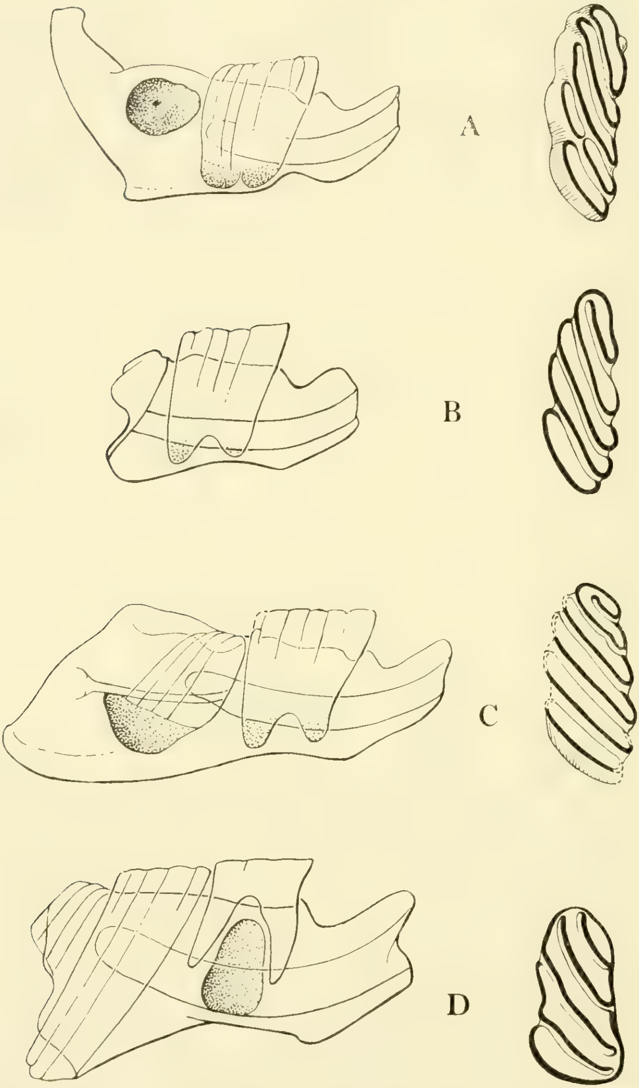


Figure 1. Early ontogeny of the lower dentition in *Elasmodontomys obliquus*, showing on the left (approximately × 1.1) immature left mandibular rami in lingual aspect, diagrammatically represented largely on the basis of X-ray photographs, and on the right (approximatey × 2.2) the corresponding DP_4 in occlusal aspect. In order of increasing age the specimens figured are: *A*, AMNH 55030; *B*, AMNH 55031; *C*, MCZ 10132; *D*, AMNH 55037.

border of the horizontal ramus), the crypt for M_1 (the thin walls of which are broken through in three places), and the base of the incisive alveolus adjacent to the posterior border of DP_4. Length of DP_4 approximately 16 mm.

AMNH 55031. Left ramus with DP_4 and M_1 (Fig. 1B). Symphysis open. Bone porous. DP_4 with five columns, the first two confluent anterolabially, the last two merging lingually 2.6 mm proximal to occlusal surface. Occlusal surface near its maximum area. M_1 apparently just at point of eruption; its columns open proximally. Incisive alveolus terminating adjacent to middle of M_1. X-ray photograph shows DP_4 with well formed double roots. Length of DP_4 slightly less than 15.8 mm.

MCZ 10132. Left ramus with DP_4 and M_1 (Fig. 1C). Age apparently comparable to AMNH 55031. Symphysis open. Bone porous. DP_4 with six columns, the first of which is subsidiary and confluent anterolabially with the second, with which it merges lingually 3.5 mm proximal to occlusal surface. Length of DP_4 less than 17 mm. Discovery that DP_4 was loose in its alveolus made possible direct confirmation of the interpretation of the X-ray photographs which indicated well-formed double roots, and in addition revealed that the posterior root is subdivided transversely into two rootlets. M_1 is just at the point of eruption but quite unworn, revealing minor subdivisions near the apices of its unworn columns which would have been expressed ephemerally at early stages of wear as isolated islands and as constrictions in the characteristic ellipses. There are four major columns with a fifth, anterior, minor one confluent anterolabially with the first major one. Incisive alveolus terminating adjacent to middle of M_1.

AMNH 55037. Left ramus with DP_4, M_1, and M_2 (Fig. 1D). Symphysis open. DP_4 deeply worn, with all five enamel columns confluent and the trace of the enamel a complex but continuous line on the occlusal surface. The occlusal area is much reduced. The tooth apparently has slipped partially out of its alveolus and subsequently become cemented in that position, revealing the bases of two strongly developed roots with the saddle between them only 4.8 mm below the occlusal surface. Including the long roots, the tooth is no less than 13 mm long. A small hole inside the alveolus between the roots of DP_4 opens into a large crypt for P_4. No trace of P_4 itself was detected. M_1 is in full use, its enamel sheaths confluent at their exposed proximal ends indicating termination of enamel growth; no trace of root formation. Length of M_1 is 32.1 mm. Longitudinal axis of M_1 widely divergent from crypt of P_4, directed posteroventrad at angle of about 60° to occlusal surface, extending into angular process to the ventral border. M_2 at point of eruption, unworn, consisting of four columns open at their bases, maximum length 15.6 mm. Incisive alveolus terminating adjacent to posterior margin of M_1.

AMNH 55041. Left ramus with M_2 and alveoli of P_4 and M_1. Symphysis tightly fused dorsally but open ventrally. P_4 alveolus very deep, producing prominent bulge on ventral border of jaw. The alveolus has a small concavity on its anterior wall near the alveolar border, which may be the vestige of the alveolus of the anterior root of DP_4, suggesting shedding of DP_4 only slightly prior to the stage here represented. M_2 is in full use, its columns confluent proximally indicating cessation of their growth. The tooth slopes posteroventrad so that its occlusal surface is highly oblique to its longitudinal axis. The base of the tooth lies posteroventral to the mandibular foramen. There is no external indication of M_3, but there is sufficient space that the crypt and tooth primordium could be accommodated. The specimen has not been X-rayed. Incisive alveolus terminates adjacent to middle of M_2.

AMNH 17137 h. Right ramus with P_4-M_3. Figured by Miller (1929, pl. 4, fig. 1, 1a). P_4-M_2 in full use, whereas M_3 is not erupted. Incisive alveolus terminating adjacent to middle of M_2.

The growing tip of the lower incisor of *Elasmodontomys* extends with increasing age progressively posterad, as far as the middle of M_3 in the oldest observed jaw (AMNH 55039). A similar sequence occurs in *Dinomys*. In the youngest observed individual (AMNH 100011, M_2 in initial wear) the tip lies at the posterior edge of M_2; in AMNH 100053 (M_3 erupting), at the posterior edge of M_3; in AMNH 46551 (DP_4 much worn), well behind M_3. No such progression occurs in *Dasyprocta;* in individuals with only DP_4 in use the growing tip of the incisor already extends posteriorly almost to the mandibular foramen.

Anthony (1918, p. 399) considered that, "the [pre-] molar of *Heptaxodon* is a logical development from a tooth like that of *Elasmodontomys* in which genus a tendency toward multiplication of the laminae of the individual tooth has been noted, this increase in number of plates being accompanied by an apparent decrease in the number of the teeth." These differences are here shown to be ontogenetic rather than phylogenetic. The differences in number of columns and in the related shape of occlusal surface between DP_4 ("*Heptaxodon*") and P_4 in *Elasmodontomys* are analogous to those between the same two teeth in *Dasyprocta*, *Cuniculus*, and *Dinomys*. The "*Heptaxodon* molar" (DP_4) has five (six in MCZ 10132) enamel loops on its triturating surface as compared to four loops in P_4 of *Elasmodontomys*. In correlation with its greater number of enamel ellipses the occlusal surface of DP_4 is anteroposteriorly elongate whereas in P_4 of *Elasmodontomys* it is trigonal and more nearly equidimensional. DP_4 of *Dasyprocta* has six transverse enamel units (each composed of two laminae of enamel with the intervening dentine) and is conspicuously elongate anteroposteriorly, whereas P_4 has five transverse units and is subequidimensional. DP_4 of *Cuniculus* has an anteroposteriorly elongate crown with at least four lingual reëntrants, the most anterior of which is complex, whereas P_4 has three simple lingual reëntrants, and an equidimensional crown. In *Dasyprocta* and *Cuniculus* the enamel does not form well-defined ellipses on the triturating surface as it does in *Elasmodontomys* and in *Dinomys*. DP_4 of *Dinomys* is composed of four discrete columns of enamel, as compared to three columns in P_4 (an unworn P_4 in AMNH 46551 has a small cylindrical fourth column on its anterior face which merges proximally with the adjacent column).

As might be expected, the number and configuration of the enamel ellipses or loops in DP_4 of *Elasmodontomys* (and in *Dasyprocta*, *Cuniculus*, and *Dinomys*) varies individually and with degree of wear. In AMNH 55030 (Fig. 1A) DP_4 is in the initial stages of wear, as indicated by the small area of the wear surface and by the division of the next to last enamel ellipse into two ellipses. The tooth is peculiar in the presence of a subsidiary pillar of enamel on its anterior face. The pillar is unworn but would be expressed on the wear surface by a small circle of enamel. With additional wear the area of the triturating surface would undoubtedly increase, the two ellipses unite, and the small pillar disappear, producing a crown pattern not unlike that of AMNH 55031. The condition of DP_4 in extreme wear is illustrated by AMNH 55037 in which the enamel no longer forms complete ellipses but forms one continuous trace on the wear surface. MCZ 10132 and AMNH 55031 are of approximately the same age, judging by similar gross size, wear of DP_4, development of M_1, and length of incisor alveolus. However, DP_4 has six enamel loops in MCZ 10132 and only five in the other three jaws. This additional loop can be ascribed to individual variation (perhaps as an expression of the same genetic tendency producing the small pillar in AMNH 55030) and undoubtedly would disappear with additional wear. Stehlin and Schaub (1951) referred to the "*Heptaxodon* molar" as a "frischer Prämolar," implying that the added enamel ellipses and elongate occlusal surface would be transformed by wear and (everlasting) growth into the configuration expected in P_4 of *Elasmodontomys.* That no such trend occurs is well shown by Figure 1D, demonstrating conclusively that the tooth in question is long-rooted and very nearly worn out before M_2 is erupted. The double-rooted, moderately hypsodont first molariform tooth in each jaw shown in Figure 1 is quite in contrast to the single-rooted extremely hypsodont permanent molariform teeth of *Elasmodontomys* (such as M_1 in Fig. 1D), indicating that the first tooth is deciduous. The permanent molariform teeth of *Elasmodontomys* differ from those of *Dinomys* in that they are not evergrowing, a fact which was recognized by Anthony (1918, p. 383). Anthony, nevertheless, considered the molariform teeth of *Elasmodontomys* to be rootless, although he accurately described and illustrated the deposition of cement beyond the base of the enameled portion of the teeth. To me this deposition seems to be acceptable as root formation. In none of the isolated teeth available is the root entirely closed, but none of these teeth is in an advanced stage of wear. In a fragmentary left ramus (AMNH "4") the root of a deeply worn M_1 is visible and broken in transverse section. The root is quite solid with the exception of a fine central canal. In the oldest available ramus (AMNH 55039), P_4, M_1, and M_2 are worn almost to the base of the enamel with long roots broadly exposed. M_3 is absent, but its well-preserved, conical alveolus tapers to a sharp apex clearly indicative of a closed root. The order of termination of enamel growth (and presumably also of root growth) of the molariform teeth is DP_4, M_1, M_2, P_4, M_3. That DP_4 terminates its growth first is self-evident and as expected. In AMNH 55037 (Fig. 1D), M_1 has terminated its enamel growth prior to the formation of P_4 and during the early growth of M_2. The conclusion that growth of M_2 terminates before that of P_4 is based on the advanced growth of M_2 in AMNH 55037, in which P_4 remains to be formed. The bases of all four molariform teeth are exposed in AMNH 55044 revealing that P_4, M_1, and M_2 have well-formed open roots whereas M_3 has terminated its enamel growth but formed no root. The termination of enamel growth in a given tooth seems to coincide with the initial wear of that tooth. This coincidence has been observed for DP_4 (AMNH 55030, Fig. 1A), M_1 (AMNH 55037, Fig. 1D), and M_3 (AMNH 55044). The appropriate stages for the demonstration of this feature in P_4 and M_2 are not available.

In *Elasmodontomys*, P_4 comes into use prior to M_3, as shown by AMNH 17137j in which P_4 is considerably worn and M_3 is unerupted. Anthony apparently considered this to be the established sequence in all hystricomorphs (including caviomorphs) for he concluded that the functional tooth in "*Heptaxodon*" was a fourth premolar on the basis of "the great importance in the hystricomorph tooth row assumed by the last premolar, since it always becomes functional before the last molar. . . ." (1918, p. 398). However, M_3 (and M^3) becomes functional prior to P_4 (and P^4) in *Hystrix*, *Atherurus*, *Erethizon*, *Dinomys*, *Olenopsis* (Fields, 1957, p. 327), *Dasyprocta*, and *Cuniculus*,[2] and the $P\frac{4}{4}$ are entirely suppressed in modern echimyids and capromyids and thus of course do not precede the $M\frac{3}{3}$ (Wood and Patterson, 1959, p. 301).

The overall sequence of eruption in *Elasmodontomys* is DP_4, M_1, M_2, P_4, M_3, identical to the sequence of termination of enamel growth, as might be expected. DP_4 is shed after the eruption of M_2, as shown by AMNH 55037 (Fig. 1D), and (obviously) prior to the eruption of P_4 (or technically shortly afterwards, for DP_4 may have remained functional after P_4 had thrust up between its roots, above the alveolar border, as noted below in *Dinomys*).

Tooth formation in *Elasmodontomys* apparently was very rapid. In AMNH 55030, for example, there is no trace of M_1 other than its crypt, whereas in AMNH 55031 and MCZ 10132 M_1 is well formed and on the point of eruption. The amount of wear incurred by DP_4 during this interval is only moderate.

---

[2] Individuals of appropriate age were fewer than desirable for all forms mentioned, but only in borderline cases would variation be expected to be so great as to affect sequence. One such borderline case was noted in caviids in which a specimen of *Microcavia australis* (MCZ 18995) was observed with $DP\frac{4}{4}$ and $M\frac{3}{3}$ in use, whereas a specimen of *Cavia porcellus* (MCZ 9426) and one of *C. tschudii* (MCZ 17736) have $P\frac{4}{4}$ in full use and $M\frac{3}{3}$ barely breached by initial wear.

Similarly, DP_4 in AMNH 55037 is worn almost to the base of its enamel, but P_4 remains unformed although its crypt is present. In a specimen of *Dinomys* (AMNH 46551) the left DP_4 has been broken off revealing a large P_4, the crown of which stands well above the alveolar border. The right DP_4 of the same individual is in place and much less worn than the same tooth in AMNH 55037.

The straight-line distance between the tip of the angular process and the anterior extremity of the jaw in MCZ 10132 (the only "*Heptaxodon*" jaw on which any sort of length measurement could be taken) is 54.5 mm, or about 60 per cent of the similar measurement in an adult jaw of *Elasmodontomys* (90.0 mm in AMNH "4"). In *Dasyprocta* the corresponding figures are 36.9 mm in MCZ 28091 (developmental stage comparable to MCZ 10132) and 60.0 mm for MCZ 32012, a young adult, again giving a percentage slightly greater than 60. Undoubtedly the precise correlation between these growth stages in *Dasyprocta* and *Elasmodontomys* is fortuitous, but it does indicate that the increase in gross size demanded of "*Heptaxodon*" in order for it to develop into *Elasmodontomys* is not unreasonable.

Upper Dentition of *Elasmodontomys*

Anthony concluded that AMNH 17101 should represent the type of a new genus with remarkably reduced dentition on the basis of the following premises:

1. The type palate "bears all the appearance of maturity" (1918, p. 398).

2. "The second and last tooth . . . appears to be an unworn tooth, not yet above the gum, but . . . may well be regarded as having dropped deeper into the alveolus than the normal position" (1917, p. 184).

3. "It is apparent from the fragment [of the palate] that there is room for no more than the two teeth" (1917, p. 184).

If the first observation is correct then the third furnishes valid evidence for the conclusion that the molariform teeth are reduced to two in each series, but if the palate (and the lower jaws) is that of a juvenile individual, it would not be expected to accommodate the full adult dentition. Anthony apparently did not consider the possibility that the palate (and the lower jaws) might be young enough for the functional tooth in each series to be a deciduous premolar. Although the bone of the palate is rather dense in texture, the fact that M^1 is little developed (maximum possible length 10.9 mm compared to

25-30 mm for M^1 with crown complete, but lacking root) and unerupted, and that the palatal sutures are open, clearly indicates that the specimen is immature. There is no indication that M^1 has "dropped deeper into the alveolus than the normal position." Assuredly it was not yet a functioning tooth, but was on the verge of eruption. The developmental stage of AMNH 17101, the type palate, approximates most closely that of MCZ 10132 among the lower jaws.

An ontogenetic sequence similar to that proposed here from "*Heptaxodon*" to *Elasmodontomys* occurs in *Dasyprocta*. Several young individuals of *Dasyprocta* (MCZ 28091, 34962, 34963) were observed to have in use only the well-worn deciduous fourth premolars with the first molars just at the point of eruption. This condition is comparable to that in AMNH 55031 (Fig. 1B) and MCZ 10132 (Fig. 1C). Obviously there is a considerable period in the early growth of *Dasyprocta* during which the deciduous fourth premolars constitute the entire cheek tooth battery, as in "*Heptaxodon*." In spite of this, the adults have the more orthodox formula of one premolar and three molars in each series, as in *Elasmodontomys*. DP^4 of *Elasmodontomys* is composed of seven columns of enamel, the first two of which merge labially less than one mm proximal to the occlusal surface, and the last two of which are confluent lingually at the occlusal plane and merge labially as well about two mm proximal to it. Just as in the lower dentition, DP^4 in *Dasyprocta, Cuniculus, Dinomys*, and *Elasmodontomys* has a longer occlusal surface made up of more units than does P^4. In the upper dentition of *Elasmodontomys*, both DP^4 (with seven) and P^4 (with five) have more enamel columns than their inferior counterparts (DP_4 with five or six, P_4 with four).

Unfortunately, documentation for dental succession is less satisfactory for the upper dentition than for the lower. However, it is clear from AMNH 17101 that DP^4 only is in use for a considerable period in early ontogeny, and that it is followed in eruption by M^1. The next stage represented is that of AMNH 17132 with P^4-M^2 in use on either side and without trace of M^3 or space for its development. Anthony (1926, pp. 108-109) tentatively interpreted this specimen as an example of evolution by discontinuous variation, supposing that the molars were reduced to two, and that the occlusal length of P^4-M^2 was increased to compensate the suppression of M^3. In fact, the occlusal length of each molar is near its maximum at the ontogenetic stage here represented, as the shaft of each molar is directed strongly posterodorsad so that the occlusal surface intersects it at a highly oblique angle. In addition, the enamel columns of all cheek teeth in this specimen have undergone postmortem separation, which has exaggerated their apparent occlusal length. Anthony felt that eruption of $M\frac{3}{3}$ in *Elasmodontomys* was unusually late in ontogeny for a "hystricomorph," indicating a tendency toward suppression. He contrasts the condition with that in *Hydrochoerus* and *Capromys,* unfortunately each representative of a group highly precocious in dental ontogeny. AMNH 17132 is here regarded as a normal stage in the ontogeny of *Elasmodontomys,* indicating that P^4 precedes M^3 in development. AMNH 55047 is only slightly more advanced than 17132, having P^4 well worn and M^3 in an early formative stage. A specimen of *Cuniculus* (MCZ 31823) represents a similar developmental stage, having $DP\frac{4}{4}$-$M\frac{2}{2}$ in use, with $M\frac{2}{2}$ newly erupted and little worn, and tiny (each less than 2 mm in diameter), superficial crypts for $M\frac{3}{3}$ present behind $M\frac{2}{2}$. No doubt this individual would have attained the full adult dentition, had it survived.[3] Definite evidence on tooth sequence in the upper dentition of *Elasmodontomys* is lacking only for the relation between M^2 and P^4. With only this point unsupported by specimens, the sequence may be given as DP^4, M^1, M^2, P^4, M^3.

The peculiar spatial relationships among the developing upper incisor, DP^4, and P^4 require special attention. In the type specimen of "*Heptaxodon bidens*" (AMNH 17101) the incisive alveoli, partially filled with matrix, terminate directly above DP^4. In specimens of *Elasmodontomys* with P^4 in use, the growing tip of the incisor intrudes between the shafts of P^4 and M^1. The shafts of the molars lie parallel to one another and are directed posterodorsad from the occlusal surface, whereas the shaft of P^4 extends anterodorsad from the occlusal surface. In old individuals (e.g. AMNH 17129) the alveolus of P^4 comes to lie shallowly under the surface of the rostrum, below the incisive alveolus. Unfortunately, growth stages between the juvenile AMNH 17101 and specimens with P^4 already functioning are not represented. These stages should be interesting developmentally as it is impossible to suppose that sufficient space could exist between the roots of DP^4 and the base of the incisor for the formation of the hypsodont P^4.

---

[3] Schreuder (1933, p. 252) has also questioned Anthony's interpretation of AMNH 17132 and compared it to immature *Cuniculus.*

I would expect to find the crypt for the developing P^4 anterodorsal to DP^4, not directly dorsal to it. X-rays of AMNH 17101 have not been altogether satisfactory owing to the superposition of images from right and left sides of the specimen, but small crypts are indeed present in the expected position just anterior to the infraorbital foramen and adjacent to the premaxillary suture. No suggestion of a cavity is present immediately dorsal to the base of DP^4.

Lower Dentition of *Amblyrhiza*

Evidence on sequence of eruption in *Amblyrhiza* is limited to a single fragmentary left mandibular ramus in matrix (AMNH 55036). The cheek teeth are represented by vestiges of DP_4, a fully-formed but unerupted P_4, and fragmentary M_1 and M_2. P_4 extends proximally at least to the ventral margin (external curve) of the incisive alveolus, a minimum length of 21 mm. The distal extremity of the tooth has been broken off level with the alveolar border, but clearly very near its tip. The three separate enamel columns are of reduced size on their broken ends, and the middle column is subdivided, with a circular island at the labial extremity of its broken end — both features indicative of a fresh, unworn tooth. Immediately anterior to the alveolus of P_4 is a small, matrix-filled circular excavation about 3.4 mm in diameter, and immediately posterolingual is a shallow elongate one about 3.3 mm in anteroposterior diameter, and 1.8 mm in transverse diameter. These are undoubtedly the alveolar sockets for the roots of a deeply worn DP_4, which may have been lost after death or shed shortly prior to death. A specimen of *Chinchilla* (MCZ 7276) has a shallow pit anterior to and confluent with the alveolus of P_4 on either side of the mandible. A specimen of *Cuniculus* (MCZ 31752) has DP_4 in use on both sides, but in a very advanced state of wear, with much basal resorption. Right DP_4 is kept in place mainly by its anterior root, the posterior ones having been largely resorbed. The distal tip of P_4 extends above the alveolar border beneath the deeply worn DP_4. In another specimen of *Cuniculus* (MCZ 32078) P_4 is in use, but immediately anterior to it on either side is a shallow, transversely elongate depression which on the left side retains a small peg of DP_4. These specimens are, respectively, slightly younger than and slightly older than the jaw of *Amblyrhiza* in relative age.

The molars in AMNH 55036 are highly fragmentary. The remnant of M_1 does extend high above its alveolar border, and must have been functional. M_2 is broken away at the alveolar border, but its base is fully exposed (though broken) revealing that enamel growth was complete. The preserved portion of the tooth is 38.8 mm long and extends to the ventral border of the jaw. M_2 must have erupted, as indicated by its advanced development and unconstricted alveolar border. Its developmental stage lies between that of AMNH 55037 (Fig. 1D) and AMNH 55041 in *Elasmodontomys.* It is probable that the sequence of eruption was DP_4, M_1, M_2, P_4, and M_3 in *Amblyrhiza,* just as in *Elasmodontomys.*

As in *Elasmodontomys,* the shafts of the molars are directed posteroventrad, diverging proximally from the more nearly ventrally directed shaft of P_4. In older jaws of *Amblyrhiza,* the incisive alveolus extends well beyond the posterior margin of M_3.

Upper Dentition of *Amblyrhiza*

The only specimen significant for the ontogeny of the upper dentition is an isolated right DP^4, AMNH 55035 (Fig. 2). The tooth is regarded as deciduous on the basis of its small size (maximum length 19.8 mm), completed enamel deposition, and anteroposteriorly elongate occlusal surface composed of five units rather than four (upper) or three (lower) as in $P\frac{4}{4}$. It is identified as DP^4 rather than DP_4 on the basis of the curvature of its shaft.

At the wear stage represented, the occlusal surface is characterized by five flattened ellipses of enamel. The first three are distinct from one another and from the fourth, but the fourth is broadly confluent with the fifth, a subcircular loop set off from the fourth only by shallow lingual and labial reëntrants. The fourth and fifth columns would have merged with much less than one millimeter of additional wear. The labial reëntrants separating columns are all quite shallow, extending proximally a maximum of 2.5 mm in the first, and decreasing successively to almost nothing in the fourth. The lingual reëntrants display a more radical decrease posteriorward in proximal extent, from 11.6 mm in the first, to 5.9 in the second, to 0.6 in the third, and practically nothing in the fourth. The tooth must have belonged to a very young animal, as its occlusal surface had

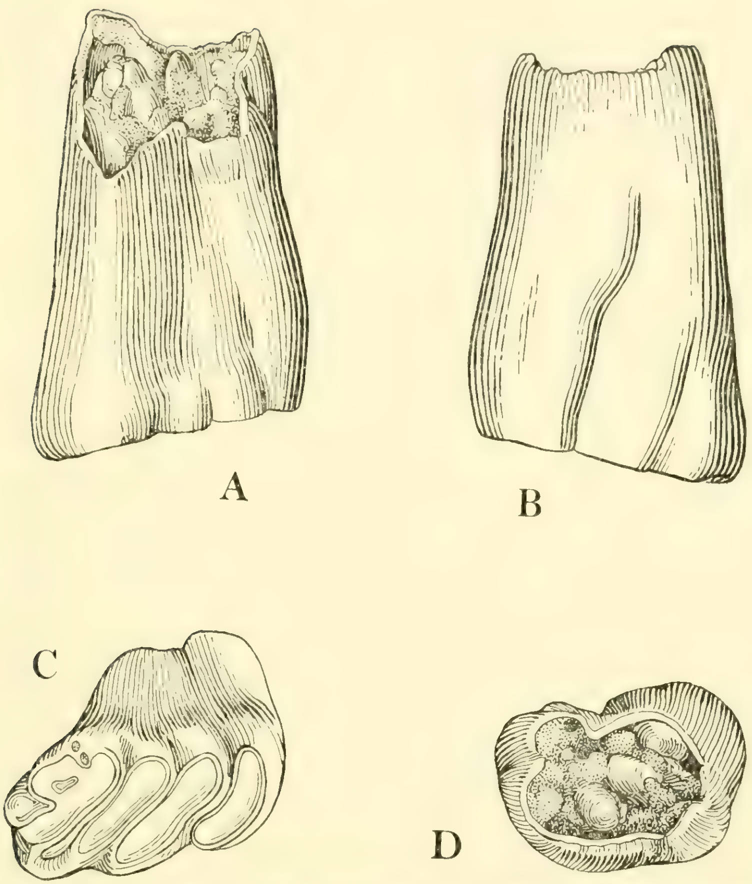


FIGURE 2. Isolated right DP^4 of *Amblyrhiza inundata* (AMNH 55035) in labial (*A*), lingual (*B*), occlusal (*C*), and proximal (*D*) aspects. Anterior is to the right in (*A*) and (*C*), to the left in (*B*) and (*D*). × 3.

yet to attain its greatest area. Breakage at the base makes it impossible to determine the status of root formation.

It may be noted here in passing that the relationship of the upper incisor to the cheek tooth row in *Amblyrhiza* is grossly different from that described above in *Elasmodontomys.* As Schreuder (1933, p. 243) has pointed out, the rostrum of *Amblyrhiza* is greatly elongated, with the upper incisor terminating far in advance of P^4, not between P^4 and M^1. I do not feel, however, that the similarity between *Amblyrhiza* and *Chinchilla* in this feature is indicative of relationship, for *Elasmodontomys* and *Lagostomus* have short rostra with the base of the incisive alveolus overlapping and closely approaching P^4, respectively.

Summary of Dental Ontogeny

"*Heptaxodon*" represents a protracted early stage in the ontogeny of *Elasmodontomys*, in which the $\mathrm{DP}\frac{4}{4}$ constitute the sole or at least dominant functional elements in the cheek tooth series. The elongate occlusal surface with increased number of laminae in the $\mathrm{DP}\frac{4}{4}$ presumably is correlated with this long period of use. The sequence of eruption, growth cessation, and root formation in *Elasmodontomys*, and in *Amblyrhiza* as far as the meager data show, is $\mathrm{DP}\frac{4}{4}$, $\mathrm{M}\frac{1}{1}$, $\mathrm{M}\frac{2}{2}$, $\mathrm{P}\frac{4}{4}$, $\mathrm{M}\frac{3}{3}$.

The growing tip of the lower incisor extends progressively farther posteriorly with increasing age in *Elasmodontomys*. The condition in *Amblyrhiza* is unknown. The growing tip of the upper incisor in *Elasmodontomys* lies directly dorsal to DP^4, leaving insufficient space for the development of P^4 in that position. P^4 develops anterodorsal to the roots of DP^4 and anteroventral to the proximal end of the upper incisor. The growing tip of the upper incisor in *Amblyrhiza* lies in the greatly lengthened rostrum, far anterior to the cheek teeth. With the possible exception of the anteriorly displaced P^4 locus, every feature in the dental ontogeny of *Elasmodontomys* has been observed in other (non-heptaxodontid) caviomorphs as well.

DISCUSSION

The West Indian genera *Heptaxodon, Elasmodontomys, Amblyrhiza, Clidomys, Speoxenus, Spirodontomys,* and (when it has been considered) *Quemisia,* have been associated in a single subfamily. *Quemisia* will be discussed elsewhere. "*Heptaxodon*" is based on juvenile specimens of *Elasmodontomys*, and is a junior synonym of the latter. I am as yet unprepared to make pronouncements on the poorly known Jamaican forms, *Clidomys, Speoxenus,* and *Spirodontomys*, and thus by default prefer to leave them, at least temporarily, in association with the present group. There is little positive evidence to support the association, but neither is there justification for placing them elsewhere in the present state of our knowledge. *Elasmodontomys* and *Amblyrhiza* assuredly are closely related, and fully warrant association at the subfamilial level. This subfamily is best regarded as a member of the family Dinomyidae, in an arrangement similar to that proposed by Schaub (*in* Stehlin and Schaub, 1951, p. 370), or possibly as a member of a family very close to the Dinomyidae (Wood, 1955, p. 182).

FAMILY-GROUP NOMENCLATURE

Anthony (1917, p. 186) proposed three monotypic subfamilies of Chinchillidae, the Amblyrhizinae, Elasmodontomyinae, and Heptaxodontinae, on successive lines of text in that order. Simpson (1945, p. 96) synonymized the three. Although Simpson neglected to mention Amblyrhizinae explicitly, his intention is clear in that he included *Amblyrhiza* in the single resultant subfamily, for which he selected the name Heptaxodontinae, a choice undoubtedly dictated by his utilization of the name Heptaxodontidae, first considered as a full family by Miller and Gidley (1918, p. 447). If subfamilial names are regarded as not influencing priority among full familial names, then Heptaxodontidae is the only valid choice. However, under the present International Code of Zoological Nomenclature (1961, Art. 23), all family-group names are regarded as coordinate for purposes of priority. In the present case, this controversial rule would have made possible the selection of a more satisfactory family name, either Amblyrhizidae or Elasmodontomyidae, both names based on older, better known genera, and as subfamilies both having line priority over the name Heptaxodontinae. Even so, Simpson, in the capacity of first reviser (International Code, 1961, Art. 24), has determined the relative priority among these simultaneously published names by selecting Heptaxodontinae as the senior synonym, and Amblyrhizinae and Elasmodontomyinae as the junior synonyms. Thus, Heptaxodontidae remains the valid name whichever system of priority is invoked. This situation is, unfortunately, not altered by the fact that ***Heptaxodon bidens*** Anthony 1917 is a junior synonym of *Elasmodontomys obliquus* Anthony 1916. The International Code (1961, Art. 40) states explicitly, "when . . . a nominal type-genus is rejected as a junior synonym, a family-group name based on it is not to be changed . . ." Thus, although there has been heated debate and strenuous disagreement on this subject, the rules are clear and ought to be followed.

The family-group name Heptaxodontinae remains available, and is not to be replaced by the name Amblyrhizinae Anthony 1917 as Schaub (*in* Stehlin and Schaub, 1951, pp. 96, 370; and 1958, p. 736) has proposed.

LITERATURE CITED

ANTHONY, H. E.

1917. New fossil rodents from Porto Rico, with additional notes on *Elasmodontomys obliquus* Anthony and *Heteropsomys insulans* Anthony. Bull. Amer. Mus. Nat. Hist., vol. 37, pp. 183-189.

1918. The indigenous land mammals of Porto Rico, living and extinct. Mem. Amer. Mus. Nat. Hist., n.s., vol. 2, pt. II, pp. 329-435.

1926. Mammals of Porto Rico, living and extinct — Rodentia and Edentata. New York Acad. Sci., vol. 9, pt. 2, pp. 97-241.

COPE, E. D.

1883. On the contents of a bone cave in the island of Anguilla (West Indies). Smithson. Contr. to Knowl., vol. 25, art. 3, pp. i-iv and 1-30.

FIELDS, R. W.

1957. Hystricomorph rodents from the late Miocene of Colombia, South America. Univ. Calif. Publ. Geol. Sci., vol. 32, no. 5, pp. 273-404.

International Code of Zoological Nomenclature. Adopted by the XV International Congress of Zoology (Ed. N. R. Stoll, Chairman, *et al.*). 1961, Internatl. Trust for Zool. Nomencl., London, xvii + 176 pp.

LANDRY, S. O., JR.

1957. The interrelationships of the New and Old World hystricomorph rodents. Univ. Calif. Publ. Zool., vol. 56, no. 1, pp. 1-118.

MILLER, G. S., JR.

1929. A second collection of mammals from caves near St. Michel, Haiti. Smithson. Misc. Coll., vol. 81, no. 9, pp. 1-30.

MILLER, G. S., JR. AND J. W. GIDLEY

1918. Synopsis of the supergeneric groups of rodents. Jour. Washington Acad. Sci., vol. 8, no. 13, pp. 431-448.

SCHAUB, S.

1958. Simplicidentata (=Rodentia). Pp. 659-818, *in* J. Piveteau (Ed.), Traité Paléont., t. VI, vol. 2, pp. 1-962.

SCHREUDER, A.

1933. Skull remains of *Amblyrhiza* from St. Martin. Tijdschr. Nederl. Dierkundige Vereeniging, ser. 3, vol. III, pt. 4, pp. 242-266.

SIMPSON, G. G.

1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., vol. 85, pp. I-XVI, 1-350.

STEHLIN, H. G. AND S. SCHAUB

1951. Die Trigonodontie der simplicidentaten Nager. Schweiz. Naturf. Ges., Paläont. Abh., vol. 67, pp. 1-385.

STIRTON, R. A.

1935. A review of the Tertiary beavers. Univ. Calif. Publ., Bull. Dept. Geol. Sci., vol. 23, no. 13, pp. 391-458.

WOOD, A. E.

1955. A revised classification of the rodents. Jour. Mammalogy, vol. 36, no. 2, pp. 165-187.

WOOD, A. E. AND B. PATTERSON

1959. The rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. Bull. Mus. Comp. Zool., vol. 120, no. 3, pp. 279-428.

(Received December 1962.)

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 6

THE SKELETON OF THE LOWER CARBONIFEROUS LABYRINTHODONT *PHOLIDOGASTER PISCIFORMIS*

By Alfred Sherwood Romer

With One Plate

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
May 25, 1964

PUBLICATIONS ISSUED BY OR IN CONNECTION WITH THE

MUSEUM OF COMPARATIVE ZOOLOGY

HARVARD UNIVERSITY

BULLETIN (octavo) 1863 — The current volume is Vol. 131.

BREVIORA (octavo) 1952 — No. 204 is current.

MEMOIRS (quarto) 1864–1938 — Publication terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 41 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 28 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained from the Publications Office of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Peters' Check-List of Birds of the World. Volumes 1, 4 and 6 are out of print; volumes 2, 3, 5, 7, 9, 10 and 15 are currently available.

Phylogeny and Evolution of Crustacea. Proceedings of a conference held at Cambridge, Mass., March 6-8, 1962. H. B. Whittington and W. D. I. Rolfe, editors. Cambridge, Mass., 192 pp., 80 figs., 1963. Cloth bound, $6.75.

Fishes of the Gulf of Maine, by Henry B. Bigelow and William C. Schroeder. Washington, viii - 577 pp., 1953. Photo-offset reprint, $6.50.

PUBLICATIONS OF THE BOSTON SOCIETY OF NATURAL HISTORY

The remaining stock of the scientific periodicals of the Boston Society of Natural History has been transferred to the Museum of Comparative Zoology for distribution. Prices for individual numbers may be had upon request.

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 6

THE SKELETON OF THE LOWER CARBONIFEROUS LABYRINTHODONT *PHOLIDOGASTER PISCIFORMIS*

By Alfred Sherwood Romer

With One Plate

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
May, 1964

Bull. Mus. Comp. Zool., Harvard Univ., 131(6): 129-159, May, 1964.

No. 6 — *The Skeleton of the Lower Carboniferous Labyrinthodont* Pholidogaster pisciformis

By Alfred Sherwood Romer

INTRODUCTION

Although the ancient labyrinthodont amphibians are of overwhelming importance in the story of tetrapod evolution, our knowledge of their early evolution and radiation is still exceedingly fragmentary. On the one hand, we are fortunate in having materials (as yet not fully described) from the late Devonian of East Greenland (Säve-Söderbergh, 1932; Jarvik, 1952, 1955) which illustrate a very early phase of amphibian history; on the other, we have a very considerable knowledge of Permian and Triassic labyrinthodonts. But most of the crucial stages in labyrinthodont evolution obviously occurred during the Carboniferous, and here our knowledge is distressingly incomplete. A fair amount of material is known from the later Carboniferous — the Pennsylvanian — but is as yet far from adequately described. Poorer still is the situation as regards the earlier — Mississippian — stage of the Carboniferous. A very limited amount of North American material of this age from West Virginia is now known and under description by Hotton and the writer. Otherwise, as reviewed by Watson (1929; cf. Panchen and Walker, 1960, pp. 327-328), Lower Carboniferous labyrinthodonts are known only from a very few specimens from Scotland, and these are mainly of a fragmentary nature.

In consequence, the type of *Pholidogaster pisciformis* Huxley is of unique importance as the only articulated skeleton of a Lower Carboniferous labyrinthodont described up to the present time. As noted by Huxley (1862), the specimen, discovered in the Gilmerton Ironstone of the Edinburgh coalfield over a century ago, was originally acquired by Sir Philip Egerton and the Earl of Enniskillen, "but as, on mature consideration, it appeared to them not to be a fish, it was handed over to the British Museum." Huxley described it briefly. Watson, in his 1929 review of Carboniferous labyrinthodonts, gave an account of such anatomical features as could then be made out. Recently Mr. A. E. Rixon has further prepared the specimen, revealing a considerable amount of new anatomical data, particularly as regards the trunk vertebrae, thus rendering further description advisable.

I wish to thank Keeper Errol I. White for the privilege of studying this important specimen. I am grateful for the friendly and helpful reception given me at the British Museum during the course of this work, not only by Dr. White but by other members of the staff, particularly Dr. W. E. Swinton and Mr. Barney Newman. And I am, of course, particularly indebted to Mr. Rixon for undertaking the preparation of this difficult material.

The specimen comes from the Gilmerton Ironstone of Gilmerton, in the Midlothian Coalfield of the Edinburgh region. As noted by Panchen and Walker (1960, p. 328), the horizon is close to the base of the Carboniferous Limestone Series. The only amphibians of greater age, apart from the ichthyostegids of East Greenland, are a few small lepospondyls and the unique *Otocratia* skull from the underlying Oil Shale Group of the Calciferous Sandstone Series of the Scottish lowlands. The amphibian remains now under study from West Virginia are from horizons near the summit of the Mississippian, and hence later in time of deposition than Gilmerton.

DESCRIPTION

Huxley's original figure shows the general character of the specimen (his pl. XI, fig. 3), although the artist has taken certain liberties with it (circular objects which he supplied in the head region suggest orbits, but the view here is ventral; the vertebral column which he pictures in the trunk region was drawn largely from his imagination, not from the material). A more accurate representation is given in my Plate I, A (in which, however, the squamation is omitted); details are shown in Figures 1 and 2. The skeleton (BMNH No. 30534) is preserved on a series of small slabs which for the most part fit together without apparent gaps; almost the complete animal was present in articulated fashion. Skull, jaws and trunk are seen in ventral view; the tail is seen from the left side. Decomposition appears to have set in to some degree before burial, so that most of the belly wall and its armor of scales, broadly visible the length of the trunk, lies mainly to the (morphological) right side of the column. The total length as preserved is 117 cm. As Huxley notes, the specimen was in "a very indifferent state of preservation," and its natural condition was not improved by preparation, a century ago, of a rather crude nature. When studied by Watson much of the structure of the tail and pelvic area was visible, as well as the surface of the under side of the head and shoulder region. Mr. Rixon's further preparation dealt mainly with the trunk vertebrae and part of the dorsal surface of the head. Since the skull is poorly preserved and little can be told of the anterior part of the body, I shall reverse the customary sequence in description, and begin with the axial skeleton of the tail, leaving skull and jaws to the last.

Tail. Nearly the complete tail is present. Parts of three vertebrae are missing in the gap between the block containing the pelvic region and those containing the rest of the tail, and another somewhat farther back where a surface chip is missing from the block. Allowing for these missing areas, thirty-one caudals are present back of the position of the presumed sacral vertebra. The tail is comparable in length with that seen in ichthyostegids, on the one hand, and various temnospondyls, on the other, but is shorter than that seen in many primitive reptiles and in the embolomere *Archeria.*

It would appear that when the specimen was discovered the slab split in such fashion that the tail was immediately exposed. However, the split ran for the most part through the substance of the vertebrae, so that surfaces of the elements are but poorly seen. The net result is that interpretation of the material is difficult. In the figures, I have endeavored to outline the structures exactly as preserved, resisting the temptation to give subjective restoration of obscure areas.

As a result of the poor condition of the material, it is difficult to tell which side of the tail we are looking at. On one margin are seen wedge-shaped neural arches from which neural spines slant diagonally backward; on the opposite margin are almost identically shaped intercentra and haemal spines. But which is which? Watson believed that the view was from the left, so that, for example, in my Plate 1, figure A the neural arches and spines lie along the lower margin. My own conclusions, based on more evidence than was available to Watson, were at first that the view was from the opposite, right, side, basing my belief on the fact that the posterior trunk vertebrae are seen somewhat to the right of a direct ventral view, and that, hence, one would expect a continuation of this twist on toward the tail. But the left half of the pelvic girdle lies uppermost and, most especially, the structure of the caudal vertebral elements is reasonably interpretable only from the Watson point

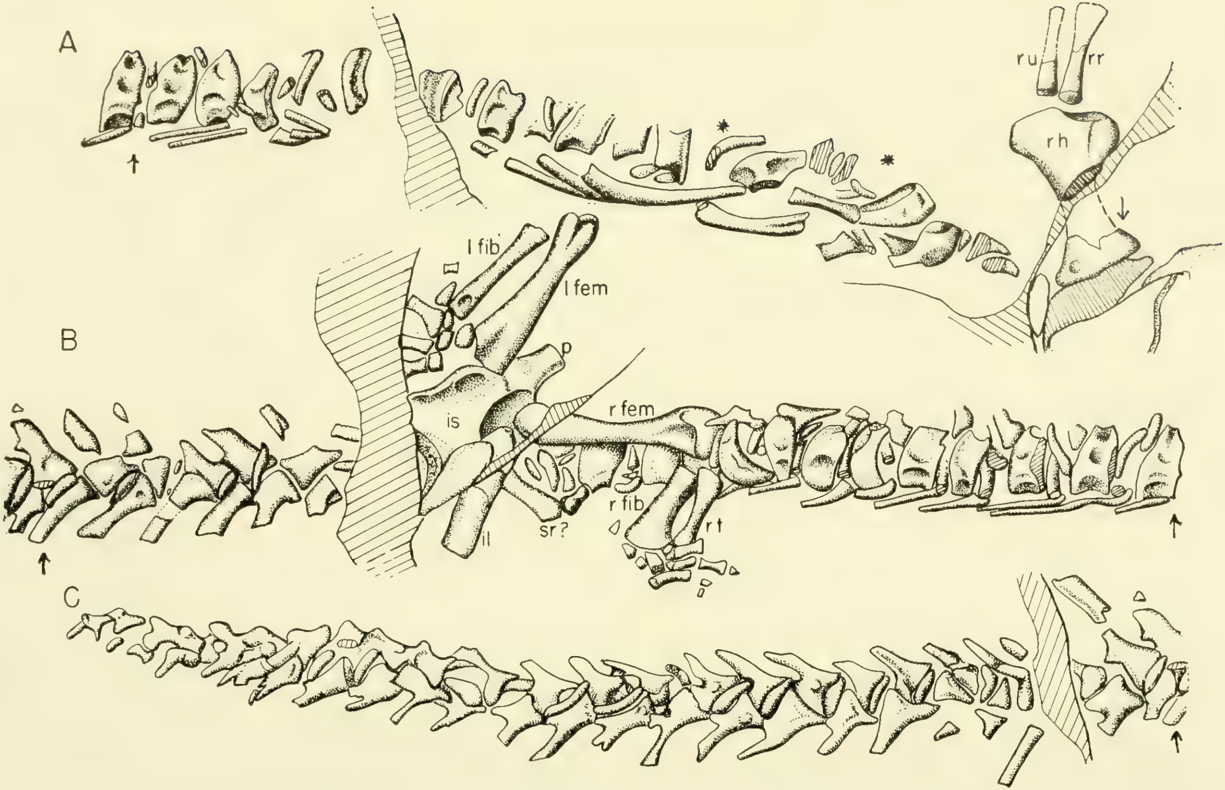


Figure 1. Successive segments of postcranial skeleton as preserved. Arrows are at identical points in successive drawings. *A*, shoulder to middorsal region; *B*, posterior dorsal, sacral and proximal caudal region; *C*, remainder of tail, × ½. Stars indicate position of centra concealed by matrix. *Abbreviations: il*, ilium; *is*, ischium; *l fem*, left femur; *l fib*, left fibula; *p*, pubis; *r fem*, right femur; *r fib*, right fibula; *r h*, right humerus; *r r*, right radius; *r t*, right tibia; *r u*, right ulna; *sr*, sacral rib.

of view. Obviously, body and tail were sharply twisted on one another at the pelvic region.

The vertebral structure of the tail, as Watson notes and illustrates (1929, fig. 7), is intermediate in character between rhachitomous and embolomerous types. Well developed neural spines are present throughout the length of the tail. They are strongly inclined backward. They were obviously flattened, and even far posteriorly are seen to be square-tipped at their distal ends where well preserved. There is some suggestion that at the tip of the tail the two arches are not fused into a single spine, but in the condition of the material this is not certain. Little can be made out regarding zygapophyses or the transverse processes which one would expect on proximal caudals.

The arch bases are massive, triangular structures, their ventral apices extending far down toward the bottom of the column. Their anterior and posterior margins are, where the surface can be clearly seen, raised ridges — the anterior margins more prominently defined — and the intervening areas somewhat concave.

The intercentra, as said above, are mirror-images of the arch bases, triangular in shape as seen in side view, with dorsal apices extending up toward the top of the central region, and with bases occupying nearly the whole length of each segment ventrally. Although nowhere is an intercentrum seen in end view, it is, as noted by Watson, improbable that a complete intercentral ring was present. Intercentra of this general type were already present in rhipidistian crossopterygians, were retained in most temnospondyls, and would be expected to be present likewise in ancestral anthracosaurians. Firmly fused with the intercentra are haemal arches which, like the neural spines, slant strongly backward. The most anterior ones are incompletely preserved, but a haemal spine appears to be present on the vertebra which I interpret as caudal two, and spines continue throughout the caudal series. Anterior ones are massively built; beyond, however, they become shorter and more slender, and in the last third of the tail are reduced to rounded swellings below the intercentra.

Most interesting of vertebral elements are the pleurocentra. When seen laterally in articulated position, the pleurocentrum is a long slender band curving diagonally downward and forward between the arch base and the intercentrum of the succeeding segment. In several instances in the tail the pleurocentra are seen somewhat out of position in the form of slender half-rings. Watson suggested that the presence of these fractional rings was due to breakage, and that in life each pair of half-rings formed a single unit, completely surrounding the notochord. However, the fact that a similar condition is also seen in several instances in the presacral column (not prepared at the time of Watson's study) strongly suggests that this ''broken'' condition is a natural one, and that in life the pleurocentrum, although completely surrounding the notochord, ossified not as a single element but as two slender hemi-cylinders. This is a condition which might be reasonably expected as an early stage in the development of an anthracosaurian column from a primitive protorhachitomous one, and is seen as an ontogenetic stage in the discosauriscid seymouriamorphs (Špinar, 1952, pp. 118-119, figs. 6-8).

Posterior trunk vertebrae. A series of vertebrae on the slab containing the posterior half of the trunk and the hind limbs is well exposed in ventral view. Unfortunately, however, the neural arches are nowhere completely preserved, and the neural spines are not visible. The intercentra are large structures, comparable to those of typical rhachitomes, 10-11 mm wide at the ventral midline and tapering gradually toward their upper ends. Anterior and posterior margins are raised rims; toward the upper ends, the narrowed lateral surface is a concave channel between the two rims. There is a rounded longitudinal ridge at the ventral midline, with a shallow pocket on each side and above each pocket a secondary longitudinal ridge. The intercentra are thin shells, and there was obviously a large persistent notochord. Little is seen of the upper termini of the intercentra. In some there is an indication of a notch in the posterior border, dorsally, for rib attachment. It was earlier believed that *Pholidogaster* was embolomerous in structure. This is not the case, for not only are the intercentra incomplete rings, but also there are no formed true centra. Instead, there are paired pleurocentra. In no instance are they here seen in place; they are displaced in various fashions, so that, fortunately, their structure can be readily made out. Each pleurocentral element, thin externo-internally and narrow anteroposteriorly, is curved so as to form an arc which in life came close, it would seem, to 180°; undoubtedly in the trunk, as can be seen clearly in the tail, the two pleurocentra came close to joining one another dorsally and ventrally. In several instances the lower end as preserved is relatively broad, the upper end slender and pointed. Presumably the lower end reached the ventral midline between successive intercentra. The upper end slanted forward along the back margin of its proper intercentrum and narrowed to allow room for the pedicel of the arch, which may have been developed somewhat as in the tail, although certainly not reaching as far ventrally.

A number of ribs are preserved. The "lumbar" ribs are straight, slender and short, typical lumbars having lengths of about 15 mm, and one farther forward (about the tenth presacral) reaching a length of 37 mm. The last precaudal intercentrum preserved lies close to the midlength of the left femur; it is a somewhat stouter element than those preceding it. On the left side its posterior margin is strongly notched near its upper end. Projecting from this notch is a stout, truncate structure which is suggestive of a sacral rib-head; close beside it, and partially concealed by adjacent materials, is a leaf-shaped structure which may well be the blade of a sacral rib.

Anterior trunk vertebrae. Remains of the "thoracic" region are visible along the "lower" margin of the first postcranial block, but were completely obscured by the dermal armor prior to development in 1960. Preparation here proved, however, very difficult. Attempts at acid preparation were fruitless; the dermal scales were closely apposed to the underlying bones and it was (and is) difficult here to tell the two materials from one another and both from matrix, and this region of the column is unsatisfactory. Nine intercentra, seen in ventral view, can be identified: they are, however, incompletely exposed and, anteriorly, somewhat disarticulated. Swellings in the scale areas covering the block suggest the presence of concealed intercentra at the points marked by stars on Figure 1 A. Pleurocentra are poorly preserved. It is, of course, impossible to determine accurately the total number of presacral vertebrae; but if the head has retained its connection with the column, the presacrals may be estimated at thirty-six — a reasonable number for a primitive labyrinthodont.

A number of ribs are seen at the lower margin of the block. None is complete. They are obviously longer and broader than the "lumbar" ribs seen on the block following posteriorly. The heads are expanded, although the nature of the articular surfaces is uncertain, and there are indications of expansion in breadth distally. One rib is preserved for a length of about 40 mm, and is obviously far from complete. No neural arches can be seen in this series.

Pectoral girdle and limb. The clavicles are exposed on their ventral surfaces.[1] They are broadly expanded ventrally, with an essentially triangular shape and with a typical labyrinthodont sculptural pattern of radiating ridges. The left clavicle is complete; the right is missing a fraction of its posterior margin. Poor remains of the sharply upturned ascending process are present on both sides. The anterior part of the interclavicle is present; it is seen between the two clavicles and a short distance back of them. The posterior part is absent, but a smooth impression, probably giving nearly the complete outline, is present on the matrix. A sculpture pattern is seen over the ventral surface of the interclavicle where visible, except posterior to the (incomplete) right clavicle, where a smooth surface for apposition with that bone is seen. The margins of this smooth area indicate that in life the two clavicles were somewhat more broadly separated posteriorly than as preserved, the right clavicle having been pushed somewhat medially and anteriorly. A slender rod seen at the margin of the slab close to the left clavicle can be reasonably interpreted, as Watson suggested, as the stem of a cleithrum. It would seem that the girdle was, in all probability, fairly comparable to that seen, for example, in *Archeria*. Between cleithrum and interclavicular impression are obscure remains obviously belonging to the left scapulocoracoid. A larger mass of broken material which presumably represents the right scapulocoracoid is seen at the (true) right-hand margin of the interclavicular impression and dorsal to the posterior end of that impression.

There are no preserved remains of the left front limb (the slab does not include the area where its remains would be expected). An impression on the matrix adjacent to the presumed remains of the right scapulocoracoid indicates the position of part of the upper end of the right humerus, but the middle portion of the bone lay in the position of the crack separating the slab containing the head from that containing the anterior end of the trunk. On this second slab are preserved the lower end of the humerus and incomplete radius and ulna; there are no traces of carpus or foot. The situation suggests a humeral length of somewhat under 5 cm; the lower end is 24 mm broad. The bone is seen from the ventral surface. There is a well developed entepicondyle, and an ectepicondylar surface separated from the under side of the entepicondylar region by a longitudinal ridge. The bone, as seen in end view, is considerably thickened above this point. There is no ossified ventral articular area for the radius, but there may have been in life a modest cartilaginous extension here. No entepicondylar foramen is seen, but the bone is somewhat crushed in the area where this might be expected.

---

[1] A comparable isolated clavicle from Gilmerton is present in the Museum of Practical Geology (no. axvii/1-5B).

The upper part of the ulna is preserved, and the distal part is represented by an impression. The olecranon was obviously unossified; the shaft was 22 mm long, the upper end 5 mm wide; the bone becomes more slender distally and the radial margin is somewhat concave. Much of the radius is present, but the lower part is incomplete, crushed and obscure. The upper articular surface has a width of 7 mm; the length appears to have been about 24 mm.

Pelvic girdle and limb. As Watson notes, considerable information can be obtained regarding the pelvic girdle and limb. There is no trace of the right half of the girdle, but the left half is present, its outer surface exposed, and the ilium directed "downward" toward the lower edge of the slab. There is the long posteriorly-directed process of the ilium common to many very primitive tetrapods (further development shows it to be broader than in Watson's figure). The region in which one would expect a dorsal iliac process for articulation with a sacral rib is damaged. Most of the outline of the acetabulum is preserved; the ischium is nearly complete; the pubis represented only by an impression.

Both femora are present, the right running forward morphologically beneath the column, the left turned upward; the left femur is seen in ventral view, the right from an anterodorsal aspect. The right femur as preserved is 46 mm in length, the left 51 mm. The width of the head is about 12 mm, the distal width the same, the slender shaft 5 mm in minimum breadth. The dorsal surface of the head, seen on the right femur, has the common pattern of primitive tetrapods: well-rounded in transverse section, and somewhat convex in outline proximally, the mid-point of the curve somewhat anterior to the line of the shaft. The exposed anterior aspect of the left femur shows the presence of a pronounced internal trochanter, with a distinct longitudinal depression developed along the anterior surface between the trochanter and the shaft proper. Unfortunately, the head region is imperfectly preserved, and little can be said except that there appears to be the usual ventral intertrochanteric fossa, bounded anteriorly by the internal trochanter. Distally, typical anterior and posterior condylar regions are readily distinguishable on both femora, the posterior, as always, more prominent. The two condyles are separated dorsally, as generally, by a distinct longitudinal hollow. Ventrally, broad articular faces for the tibia are seen, facing outward and downward at about a 45° angle; the right femur shows that the end of the posterior condyle was (as frequently in labyrinthodonts) unossified. The anterior articular surface extends some distance up the shaft. Ventrally a deeply excavated popliteal space is seen, on the right femur, between the two condyles. A low but sharp adductor crest runs proximally up the shaft from the posterior margin of the popliteal space. Presumably it connected proximally with the internal trochanter, but preservation proximally is not good. On the whole, the femur is of a generalized and primitive type of the sort seen, for example, in the *Papposaurus* femur from the somewhat later Loanhead No. 2 Ironstone (Watson, 1914) or in *Archeria.*

The right tibia and fibula are seen from the anterior (extensor) aspect. The tibia has a length of 24 mm; the head, somewhat convex in outline, is 7 mm broad; the shaft contracts to a width of 4 mm, then expands distally, where the width of the bone (partially covered by a metatarsal) appears to have been 9 mm. The fibula (as Watson notes) is, as in primitive tetrapods generally, a longer and broader bone than the tibia, with a length of the right element of 28 mm, and widths of head (partially covered), shaft, and distal extremity of 8, 5 and 11 mm, respectively. As in labyrinthodonts generally, the distal articular surface curves broadly proximally toward its tibial margin, affording contact, presumably, with a proximal centrale as well as an intermedium. On the left side the tibia is not preserved; the element present is the fibula. Its length (as is that of its mate) is 28 mm. It appears thin because seen from its medial aspect. Distally the medial portion of the articular surface is exposed.

As Watson notes, the tarsal region is difficult of determination. The left tarsus has been exposed since his studies. Preserved (partly as impressions) are a large proximal element and three more distally, above the heads of the metatarsals. Possibly these may represent an intermedium and fibulare, fourth centrale and tibiale; but if so, we must assume that the distal tarsals and more distant centralia have been displaced and were possibly unossified. On the right side is a large element which (again) I tend to identify as an intermedium, and several smaller and rather obscure elements. On either foot three articulated metatarsals are present. This count is surely due to accidents of preservation, and not improbably the animal was pentadactyl. The three left metatarsals have lengths as preserved (counting from the fibular margin) of 10, 9 and 8 mm (the second and third reach the edge of a fracture in the block and may have been slightly longer). Those of the left side (counting in the same direction) have lengths of 11, 11 and 12 mm. On the left foot a further, incomplete metatarsal is present alongside the distal end of the fibula. Both feet appear to be seen from the ventral aspect. The metatarsals are essentially flat and featureless, but there is a suggestion of a slight dorsal arching of the bones along their lengths. The most medial toe of the right foot originally had three phalanges, with lengths, as seen in Watson's drawing,[1] of about 5, 2+ and 1 mm. This toe has been partially removed, to exhibit a proximal phalanx of a second toe, 7 mm long. Beyond this, Watson's figure indicates, there was formerly a second phalanx, about 4 mm in length, and a small terminal element.

Abdominal armor. The ventral armor is well preserved over most of the region between pectoral and pelvic girdles; its general disposition may be seen in Huxley's figure 1. As typically, the rows of gastralia on either side meet at a sharp angle in the midline. This midline can be traced from a point just proximal to the entepicondyle of the right humerus back, roughly parallel to the vertebral column, to a termination anterior to the head of the right femur. Along the anterior part of the trunk the midline lies but 10-16 mm to the right of the exposed vertebral centra; in the "lumbar" region, however, the midline arches to the left, to an extreme of 40 mm from the column, before curving back toward the pelvis. The squamation of the left side curved downward over the vertebrae and ribs. This area was partly destroyed during preparation of the column. The squamation of the right side, however, is fully exposed as far as it was preserved in the specimen when collected. Along the anterior part of the column the squamation extends outward but 20-30 mm from the midline, giving the diagonally-directed scale-lines a length of 25-38 mm. It is probable that the narrowness of the squamate area preserved here is due to post-mortem loss. At the middle of the back, breadth of the scale-covered area increases, and extends out some 50 mm to the far edge of the slab, giving a maximum length of scale rows, as preserved, of about 70 mm. More posteriorly, the width of the scaled area decreases to about 20-25 mm a few centimeters in front of the pelvis; as preserved, however, the scale rows here slant very strongly backward (perhaps due to post-mortem distortion) so that their lengths approach 50 mm.

---

[1] The reduction is closer to × ¾ than to the × ⅔ given in Watson's legend.

The general pattern of arrangement of the gastralia is seen in Huxley's figure 4. However, his illustration is rather more than "of the natural size," for in general the scales are but about 10-15 mm long. They are essentially oat-shaped, with greatest widths about one-third the length. Their apparent width is less; posterior to a longitudinal ridge, the surface of each scale is overlapped by its neighbor, so that the average exposed width is little over 2 mm. As Huxley shows (but generally to a somewhat greater degree) the ends of the scales overlap their neighbors in the same scale row. The maximum number of scales in a given diagonal row does not appear to exceed ten or so, even in the broadest preserved area of squamation. The central element in each row is roughly U-shaped, with the two arms of the U diverging posteriorly from one another at about 60°; anteriorly, each median scale sends forward from its rounded central area a tongue-shaped process which underlaps its anterior neighbors.

Skull. The skull has been crushed flat in such fashion that the jaws were pushed somewhat to the right, the skull to the left. A limited amount of the dermal roof is visible on the under surface (Fig. 2). At the "lower" margin is seen a fragment containing most of the left jugal. Its posterior end is represented only by an impression, and hence its relation to the quadratojugal is not clear. The ossification center is close to the anterior end of the part preserved. Near the anterior end of the jugal are fragmentary remains of the lower margin of the left maxilla; a few small teeth are visible. The lower margins of both premaxillae are visible. The teeth are for the most part absent, but nearly the whole length (of about 7 mm) of a large tooth is preserved, and there are obscure remains of several other teeth and alveoli. Lying near the right clavicle is the displaced right quadrate, and a broken strip of bone anterior to it may be the right quadratojugal.

The dorsal surface of the skull was embedded in a mass of ironstone. At my request Mr. Rixon cleaned, with considerable difficulty, the anterior portion of this surface, revealing a series of crushed and displaced fragments. A further area cleaned, in

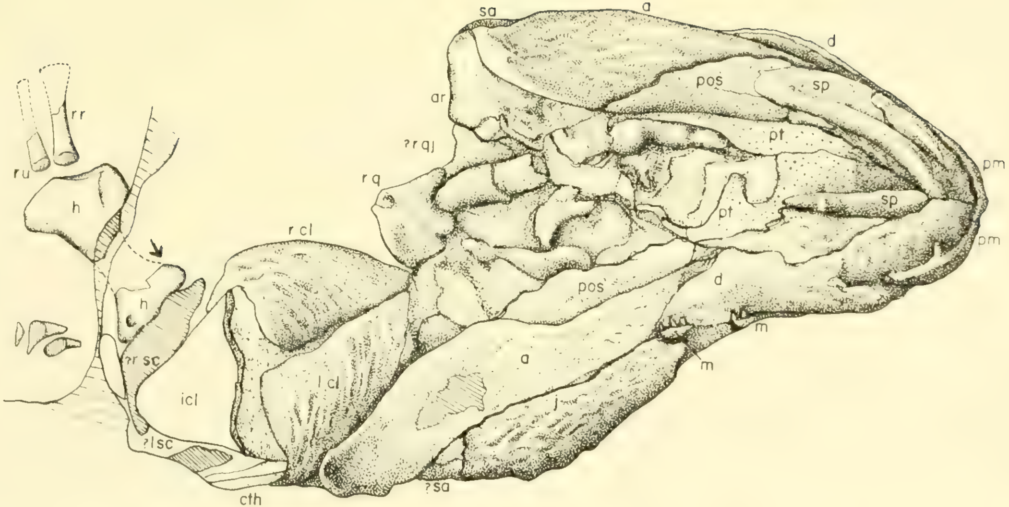

sa
a
d
pos
sp
ar
pt
?rqj
pm
rq
sp
pt
pm
rr
ru
h
r cl
pos
d
h
m
?r sc
a
m
l cl
icl
j
?lsc
?sa
cth

Figure 2. Cranial and shoulder region of the type, in ventral view. × ½. *Abbreviations: a*, angular; *ar*, articular; *cth*, cleithrum; *d*, dentary; *h*, humerus; *icl*, interclavicle; *j*, jugal; *l cl*, left clavicle; *l sc*, left scapulocoracoid; *m*, maxilla; *pm*, premaxilla; *pos*, postsplenial; *pt*, pterygoid; *r cl*, right clavicle; *rq*, right quadrate; *r qj*, right quadratojugal; *r r*, right radius; *r sc*, right scapulocoracoid; *r u*, right ulna; *sa*, surangular; *sp*, splenial.

the left posterior region of the roof, exposed a mass of crushed bone fragments impossible of interpretation, and no attempt was made to clean the rest of the roof, since it is highly improbable that the results would be worth the effort. Anteriorly (Fig. 3), the right premaxilla is apparently present in toto, and a portion of the left is seen as well. Posterior to them are good-sized sculpture plates representing much of the nasals, and to the left of the left nasal much of the left lacrimal and part of the left maxilla are preserved. A fragment posterolateral to the right premaxilla may be an incomplete right lacrimal; a tooth-bearing strip of maxilla is seen posterior to this. I cannot be sure of the nature of any of the more posterior skull roof fragments. The acid preparation has preserved the sculpture pattern in excellent style. There is little evidence of radial arrangement of the ornament, which consists essentially of subcircular pits surrounded by well-raised ridges.

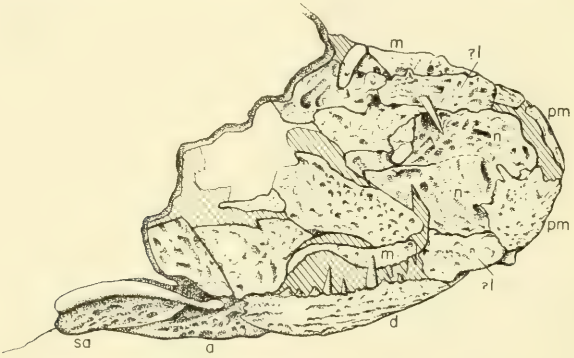


Figure 3. Dorsal view of anterior part of head of type. × ½. *Abbreviations*: *a*, angular; *d*, dentary; *l*, lacrimal; *m*, maxilla; *n*, nasal; *pm*, premaxilla; *sa*, surangular.

A considerable amount of bony material, presumably pertaining to the palate and braincase, can be seen on the ventral surface between the jaws, but little of it is interpretable. Paralleling the right jaw ramus is a long strip of denticulate bone which is presumably part of the right pterygoid, and opposite this a second dentate area presumably belonging to the left pterygoid.

Lower jaw. Nearly the entire external surface of both lower jaws is exposed on the ventral aspect of the cranial slab. The left jaw as preserved measures 186 mm from symphysis to end of articular; one gains strongly the impression that anterior and posterior portions have been pulled somewhat apart. The right jaw appears much shorter, measuring 140 mm in length as preserved, due to the fact that it was so broken post-mortem that the posterior portion has pushed forward under the anterior part. Very probably the actual length in life was on the order of 160 to 170 mm. In the left ramus the distortion is such that the splenial elements, which curved medially toward the ventral surface in life, are flattened into the plane of the angular and dentary, thus giving an impression of greater than true depth. Several fragments include most of the dentary, but nowhere is its alveolar margin present. The left surangular is nearly completely covered by a plate including most of the jugal. Over much of the posterior part of the angular region the surface is eroded. On the dorsal side (not figured) the articular surface is nearly completely visible; it is, as in many primitive forms, divided into two areas which are at nearly right angles to one another and separated by a rounded ridge. Anteromedially, there is here seen a ridge representing the posterior end of the prearticular and, below this, the thickened rounded ventromedial margin of the angular.

On the right side, as noted above, anterior and posterior segments of the broken jaw over-ride one another. The anterior segment includes splenial, postsplenial and part of the dentary. The dentary is so broken that much of its posterior portion is turned over to appear on the upper surface of the slab. Here the middle portion of the tooth row is present, although poorly preserved. Of the posterior segment, the greater part of the angular is seen on the lower aspect. At the back, crushing is such that the articular is seen in posterior view, but preservation is poor. Dorsally is seen a small portion of the angular and the overturned upper portion of the surangular, including its curved upper margin; much of the extent of this bone appears to have been lost from the margin of the slab.

Our knowledge of the lower jaws of the type is, thus, confined almost entirely to the outer surface. The pattern obviously conforms to that common to many primitive or generalized labyrinthodonts, and shows no diagnostic character of any sort.

The Edinburgh skull and jaws. Watson (1929) identified as probably belonging to *Pholidogaster* a skull in the Royal Scottish Museum (no. 150.561) which, from the character of its matrix, appears to come from the Gilmerton ironstone. I see no reason to dissent from this identification. The size and shape are appropriate. I have estimated the jaw length in the type as about 160-170 mm; the length of a jaw associated with this Edinburgh skull is 163 mm. As can be seen, the skull is diagnostically anthracosaurian, as would be expected from the "subanthracosaurian" nature of the vertebral column. The sculpture of the skull roof is more sharply defined in the type skull, but this is attributable to the acid preparation of the type, whereas the Edinburgh specimen is a split block, in which sculptured ridges are seldom sharply preserved.

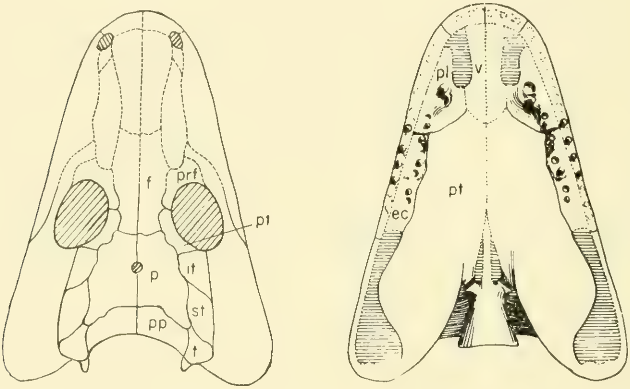


Figure 4. Dorsal and ventral views of the Edinburgh skull, modified from the restoration by Watson. *Abbreviations: ec,* ectopterygoid; *f,* frontal; *it,* intertemporal; *p,* parietal; *pf,* postfrontal; *pl,* palatine; *pp,* postparietal; *prf,* prefrontal; *pt,* pterygoid; *st,* supratemporal; *t,* tabular; *v,* vomer.

I reproduce (Fig. 4) Watson's attempted restoration of this skull, with some additions resulting from restudy of the specimen. The skull table is comparable to that of embolomeres, particularly in the fact that, as in that group, the well developed intertemporal extends forward to nearly completely separate postfrontal and postorbital. I believe the tabular-postparietal suture can be made out on the right side in approximately the position indicated by Watson. The outer margins of the supratemporal and tabulars curve downward toward the plane of the cheek, but the fact that the right cheek has broken off from the table along the plane of suture between squamosal and table indicates the presence of the zone of weakness here expected in anthracosaurians. On the right side of the facial region there are indications of part of the sutural pattern, and I have indicated sutures here (with doubt) as broken lines. It seems probable that the lacrimal was excluded from the orbital rim by a prefrontal-jugal contact. There is a break parallel to the tooth row which Watson has interpreted as the upper border of the maxilla. I rather think, however, that this break lies along the length of the lateral line groove, and that anteriorly the maxilla extended farther dorsally. I can make no more of the palatal aspect than the features shown in Watson's reconstruction.

The right lower jaw (Fig. 5) is completely preserved as to length, but crushed and partially covered by the skull. It is slender anteriorly, gradually deepening posteriorly. Little can be made out regarding the external surface except that anteriorly, where the inner surface of the jaw is missing, there can be seen indications of sutures between the dentary and a narrow splenial and, more posteriorly, a second splenial element. The inner surface is preserved posteriorly. There is a strong medial process extending inward below the articular region, apparently corresponding to the region seen in ventral view as part of the crushed right jaw of the type. The inner face of the jaw below and anterior to the articular region is deep; its upper margin, forming the inner rim of the adductor fossa, bears a low but definite ridge. Farther forward, little can be made out of the inner jaw aspect, but enough is present to show that the large fossae in this region which are characteristic of embolomeres were not present.

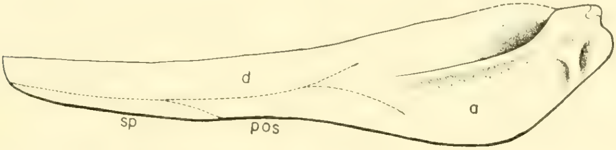


Figure 5. Inner view of the right mandible of the Edinburgh specimen. Anteriorly, the inner surface is absent, so that indications of sutures of elements of outer surface are seen. × ½. *Abbreviations: a,* angular; *d,* dentary; *pos,* postsplenial; *sp,* splenial.

Lower jaw teeth are not seen, but maxillary teeth are present. As in the type they are numerous, small and slender; when completely preserved they are seen to be slightly recurved at their tips, and there is some indication of striation in the basal part of the teeth. They are spaced 3.5 to 4 mm apart. It would appear that replacement was actively underway at the time of death, with empty alveoli between most of the teeth present. There is no indication of a developed canine region, but such teeth as are well preserved suggest a region of maximum length of about 10 mm at a point somewhat anterior to the midpoint of the maxilla. Presumably the tooth row (including empty alveoli) included (as Watson's figure suggests) about 30 teeth.

DISCUSSION

Restoration. Because of the unique nature of this skeleton, I have thought it worth while to attempt a restoration — this despite our inadequate knowledge of certain features (Pl. 1, B). Uncertainties regarding skull structure have been noted earlier. The endochondral shoulder girdle and cleithrum are incompletely known, but it is reasonable to restore these elements according to the common pattern found in forms removed as far from one another as the embolomere *Archeria* and the rhachitome *Eryops*. The manus is missing, the ribs are incompletely known, and few data are available regarding presacral neural arches, but we cannot go far wrong in restoring absent elements in the fashion common to most labyrinthodonts. With his short limbs, long trunk and well developed tail, *Pholidogaster* was, obviously, primarily a water-dwelling form as, presumably, were all primitive labyrinthodonts.

Phylogenetic position of Pholidogaster. In many regards *Pholidogaster* is a rather generalized and essentially primitive labyrinthodont. The specimen is well ossified and obviously mature. With a length of about 117 cm — less than four feet — it is a much smaller animal than such well known Carboniferous labyrinthodonts as the large embolomeres of the *Pteroplax-Eogyrinus* group and such a large loxommid as *Megalocephalus*. On the other hand, it is not far from the size of the ancient ichthyostegids, and labyrinthodonts with proportions similar to those of *Pholidogaster* occur at various later levels of the Carboniferous.

Apart from the vertebral centra, the postcranial skeleton shows few diagnostic features. The broadly triangular clavicular plates are presumably primitive in character. Such plates are characteristic of embolomeres and seymouriamorphs in later times, but broad clavicular plates are present in some seemingly primitive temnospondyls (as well as advanced forms) and are seen in the archaic ichthyostegids. The interclavicle is unfortunately incomplete; it was obviously long, but elongation is found in some temnospondyls as well as in anthracosaurs, and one cannot tell whether or not the long stem essentially diagnostic of the later group was present. The ilium shows a long posterior process plus, apparently, the small ascending blade for sacral rib articulation. This structure has long been recognized as one found in the embolomeres and such further anthracosaurians or seymouriamorphs as *Diplovertebron* and *Discosauriscus*. But since we now know that this type of ilium was already developed in ichthyostegids, this feature, again, is not a diagnostic one. Too little is known of limbs in early labyrinthodonts to make profitable an attempt at diagnosis on the basis of limb bones.

The vertebral structure, however, is almost unique. As described above, the intercentra are the prominent elements of the central region — massive structures, although incomplete dorsally, which form the main supports of the neural arches. The pleurocentra have the form of paired half-rings, surrounding the notochord; they are slender but extend the full depth of the central region.

It is entirely reasonable to assume that the vertebral structure of *Pholidogaster* represents an initial stage in the development of the anthracosaurian vertebral column, leading to the structures present in embolomeres, seymouriamorphs and typical reptiles.

Because of the prominence of the embolomeres in collections of Carboniferous amphibian materials, it was at one time assumed that this type of vertebral structure was a basic one for labyrinthodonts; that there had been derived from this, on the one hand, the rhachitomous and stereospondylous types, in which pleurocentra became reduced and the intercentrum became dominant, and, on the other hand, a series in which the ring-shaped embolomerous intercentrum was progressively reduced, thus leading to seymouriamorphs and reptiles.

It has, however, become apparent in recent decades that the embolomeres were far from being the sole labyrinthodonts in the Carboniferous. It now seems clear that, despite their retention of a number of primitive features, the embolomeres are merely a subgroup of one of the two major lines of labyrinthodont evolution — the Anthracosauria; a parallel radiation of rhachitomous forms was also taking place during the Carboniferous.

As a result, I proposed in 1947 an alternative scheme of labyrinthodont evolution — one in which the ancestral type possessed vertebrae which were not embolomerous but proto-rhachitomous

(Fig. 6). Typical crossopterygians, from which labyrinthodonts may be reasonably derived, have in many instances large wedge-shaped intercentra and very small paired pleurocentra, situated dorsally near the lower margins of the neural arch. To develop from this the temnospondylous type of vertebra seen in the Rhachitomi requires no change except some modest increase in the size of the pleurocentra to strengthen the column by filling

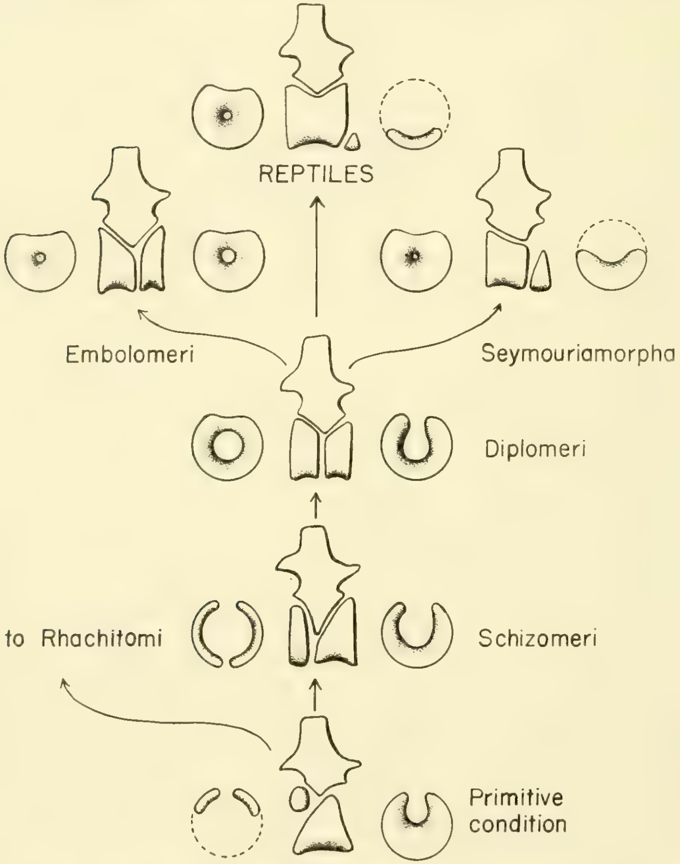

REPTILES
Embolomeri
Seymouriamorpha
Diplomeri
to Rhachitomi
Schizomeri
Primitive
condition

Figure 6. Suggested evolutionary series of anthracosaurians, with a typical vertebra representing each stage or group. In each case the vertebra as a whole is seen from the right side; at the left the pleurocentra (or centrum) shown in end view; at the right, the intercentrum in end view.

out the gaps in the dorsal part of the central region where ossification had been lacking. To develop an anthracosaurian type of vertebra would demand a major development of the pleurocentra. They should expand and coalesce to form a ring-shaped true centrum. Beyond this stage, completion of a ring-shaped structure of the intercentrum as well would lead to the embolomerous condition as a side line; on the other hand, reduction of the intercentrum would lead to the conditions seen in seymouriamorphs and typical reptiles.

Support for this theory of vertebral evolution was given by Jarvik's description (1952) of the vertebral column of ichthyostegids. In them, as in many crossopterygians, the pleurocentra are very small, dorsally placed, paired elements. To be sure, the ichthyostegids are probably somewhat off the main line of labyrinthodont evolution, but the presence here of proto-rhachitomous vertebrae is strongly suggestive of the general scheme of vertebral evolution which I had advocated.

Further support of this theory is afforded by the vertebral condition of *Pholidogaster*. If we are to form a true centrum from the small, dorsally placed pleurocentra of an ancestral crossopterygian, downward growth, toward the bottom of the column, of these paired elements is the first change to be expected — this to be followed later by a fusion of the two pleurocentra into a complete, true central, ring. This theoretically expected stage is perfectly exemplified in the two half-rings of the *Pholidogaster* centrum. The assumption that this condition is phylogenetically antecedent to the formation of a true centrum is reinforced by the ontogenetic condition described by Špinar (1952, pp. 118-119, figs. 6-8) in the seymouriamorphan family Discosauriscidae. Here the larger specimens show a complete true centrum; but smaller and more immature individuals show paired hemicylinders corresponding closely to those of the mature *Pholidogaster*. In the older individuals the two hemicylinders fuse ventrally and, still later, dorsally, to complete the mature central structure.

Although the attribution of the Edinburgh skull to *Pholidogaster* is not capable of absolute proof, the phylogenetic implications of the structures seen in this skull are in perfect harmony with those derived from vertebral structure. The proto-anthracosaurian build of the *Pholidogaster* vertebrae call for the presence of a skull with anthracosaurian attributes; the definitely anthracosaurian nature of the Edinburgh skull calls for a vertebral column of anthracosaurian or proto-anthracosaurian build.

That the Edinburgh skull is anthracosaurian cannot well be doubted. The tabular "horns" are of modest size, and are not, as Panchen and Walker (1960) have pointed out, of the long, pointed embolomere type; such structures are quite surely specializations of the embolomeres, and not to be expected in generalized anthracosaur ancestors of seymouriamorphs and typical reptiles as well as embolomeres. Four diagnostic features may be expected in the skull of an ancestral anthracosaurian: (1) A tabular of good size which, as emphasized by Säve-Söderbergh (1935) and Steen (1938), articulates with the parietal — this in contrast to the reduced tabular of temnospondyls. Such a tabular is present in *Pholidogaster*. (2) A loose attachment of cheek to skull table with, posteriorly, a wedge-shaped otic notch. Current (and reasonable) belief as first advocated by Watson (1926) is that this is a primitive situation, retained from the fish stage; later anthracosaurians leading to seymouriamorphs and typical reptiles have modified this structure, but it is characteristically retained in embolomeres. In theory, the ancestral temnospondyl may have had this structure as well, but fusion of cheek and table and development of a rounded rather than a wedge-shaped otic notch obviously occurred at an early stage in temnospondyl evolution. The Edinburgh skull is primitive in construction, but the Gilmerton deposits are fairly well up in the Lower Carboniferous, and the time element speaks strongly for the Anthracosauria here. (3) In rhachitomes, postfrontal and postorbital are broadly connected back of the orbit, and the intertemporal, when present, is widely separated from the orbital rim. In embolomeres, in strong contrast, the intertemporal pushes toward the orbit so that there postfrontal and postorbital barely touch one another. In reptiles the intertemporal is normally absent and in seymouriamorphs it is reduced, so that a fair area of postfrontal-postorbital contact is developed. But the contact is still narrow in many seymouriamorphs and the embolomere condition may be reasonably regarded as primitive for anthracosaurians. The *Pholidogaster* intertemporal is emphatically of the type of the presumed anthracosaurian ancestor. (4) In all typical rhachitomes, including the loxommids (and in the ichthyostegids as well), the muzzle is broadly rounded and on the palatal aspect the nares are widely separated, with between them broad plate-like vomers bearing a prominent tusk-pair. In embolomeres, in contrast, the nares are close together in the narrow snout, separated only by narrow strap-shaped vomers which lack tusks. Primitive reptiles show this same condition, which can hence be reasonably regarded as primitive for anthracosaurians. This pattern is present in the Edinburgh skull, further reinforcing belief as to its pertinence to the Anthracosauria. Too great reliance, however, should not be placed on this last feature, for it is obviously correlated in considerable measure with snout shape, and seymouriamorphs with broadly rounded muzzles approximate the rhachitome condition.

In sum — the vertebral construction of the type and diagnostic features found in the Edinburgh skull indicate that in this Gilmerton amphibian we are dealing with a primitive member of the anthracosaurian group of labyrinthodonts.

Labyrinthodont classification. In 1947 I reviewed the Labyrinthodontia at some length, and established a classification based on all evidence then available. A major cleavage was made into two groups: Temnospondyli (including typical rhachitomes and stereospondyls, the loxommoids and ichthyostegids) and Anthracosauria (including the embolomeres and forms leading to reptiles, with the semouriamorphs dangling, so to speak, on the amphibian-reptilian boundary). This dichotomy was based to some degree upon cranial characters of the sort discussed above, but primarily on divergence in vertebral structure — continued emphasis on the intercentrum among the temnospondyls, in contrast to a strong trend among anthracosaurs toward development of a typical centrum from the tiny paired pleurocentra of ancestral forms.

Various advances made during the decade and a half since this essay at classification suggest that reappraisal of the situation may be in order. The basic concept of a division into temnospondyls and anthracosaurians appears to have been reinforced by later discoveries, including the presence of proto-rhachitomous vertebrae in the ichthyostegids, as noted above, and of rhachitomous vertebrae in the previously doubtful loxommids (Baird, 1957).

Perhaps the one advisable major change would be the separation of the Ichthyostegalia as a third, minor but distinct, labyrinthodont group. To be sure, my inference that their vertebrae were rhachitomous has been validated, and they agree with the temnospondyls rather than anthracosaurians in fusion of cheek and braincase, a rounded otic notch, and broad vomers. But even Jarvik's preliminary descriptions show such a series of primitive characters that it is difficult to associate the ichthyostegalians closely with the more advanced temnospondyls of later times. Further, currently accepted tenets assume that the intertemporal was part of the ancestral skull pattern of labyrinthodonts; its absence in the ichthyostegids suggests that they were, even at this early stage, somewhat of a side line. Accordingly, it is perhaps preferable to consider the ichthyostegal forms as a third, distinct group of labyrinthodonts, as follows:

Superorder (or Subclass) Labyrinthodontia
    Order (or Superorder) Ichthyostegalia
    Order (or Superorder) Temnospondyli
    Order (or Superorder) Anthracosauria

I shall refrain here from discussion of the temnospondyls, although work being done at present, by Baird and Carroll, for example, suggests progress toward sorting out true phyletic lines among the Rhachitomi in preference to the somewhat artificial grouping which I used in my 1947 classification. With regard to the ichthyostegalians, it is possible that with further knowledge the East Greenland forms will prove to be but one, possibly aberrant, subgroup of an archaic group which will also include forms more directly ancestral to later temnospondyls and anthracosaurians.[1] It is pleasant to find that my suggestion (put forth in 1945) that *Otocratia* is related to the ichthyostegids is supported by the finding of a comparable otic construction in an East Greenland genus (Jarvik, 1952). However, my further suggestion that the colosteids of the Pennsylvanian are much evolved ichthyostegids has not gained support either from new materials or from the opinions of my colleagues.

Our present concerns are with the anthracosaurians (Fig. 6). As I pointed out in 1947, the major evolutionary event in early anthracosaurian history must have been the development of a complete ring-shaped centrum from the primitive, small, paired, pleurocentral elements, the intercentrum remaining persistently large. Once the true centrum evolved, further evolution could have proceeded in two directions — on the one hand, to the embolomeres with development of a ring-shaped intercentrum, and, on the other, to seymouriamorphs and typical reptiles with reduction of the intercentrum. In *Pholidogaster* we have a half-way stage in the development of a centrum, with the ring completed spatially, but consisting of two discrete, pleurocentral halves. At the moment there is no other typical anthracosaurian known to me which has such a structure as an adult, although rather surely *Pholidogaster* had predecessors, contemporaries and possibly successors exhibiting this structural stage. As noted earlier, Špinar (1952, fig. 6, etc.) figures specimens of *Discosauriscus* (*Discosaurus*) in which the centrum is in the form of two ''pleurocentral'' half-rings, and Credner (1893) also figures this condition. However, as Špinar clearly demonstrates, we are here dealing with larval forms; the adult was a seymouriamorph, in which there was a complete central ring.

---

[1] I am sometimes tempted to speculate that the ichthyostegid skull pattern may be related to the peculiar arrangement seen in microsaurs, but there is, of course, not the slightest positive evidence for such a belief.

Despite the lack of known relatives, it seems reasonable to consider *Pholidogaster* as representative of a stage in anthracosaurian evolution which may be reasonably termed the suborder (or order) Schizomeri — the name referring to the ''broken'' appearance of the pleurocentral ring.

Vertebrae with a construction of this same sort are described by Eaton and Stewart (1960) in *Hesperoherpeton*, a tiny amphibian from the Pennsylvanian of Kansas. They consider this form as the type of a new order, the Plesiopoda. I hesitate, however, to use this term for the stage in anthracosaurian evolution represented by *Pholidogaster*. The skull of *Hesperoherpeton*, as described by Eaton and Stewart, departs wildly not only from that of the anthracosaurians but from that of any known labyrinthodonts; the pectoral limb is equally aberrant and seemingly primitive and fish-like, and the ordinal term has reference to foot structure, not to vertebral type. Possibly *Hesperoherpeton* is a larva whose metamorphosed adult would have had a more normal labyrinthodont structure; again, this form may represent an aberrant side branch from the schizomeran stage of anthracosaur evolution; still again, it may represent an independent group developed from ancestral forms in parallel fashion to the anthracosaurs as regards vertebral structure.

Next above the schizomeran level should be one in which the two pleurocentra should have fused to form a complete ring centrum, but in which there persisted an intercentrum incomplete dorsally, but still retaining full height from the bottom level of the column to an articulation with the neural arch. Certainly, considering the radiation in the later Carboniferous of embolomeres, seymouriamorphs and true reptiles which developed from forms in this structural stage, animals of this sort must have evolved before the close of the Mississippian.

There are, however, few described specimens which appear to fall in this category. Somewhat comparable vertebrae from the Upper Carboniferous Joggins tree stumps of Nova Scotia occur on a slab containing a fragmentary skull described by Steen as *Dendryazousa* (Steen, 1934, fig. 17). As described, however, this skull fragment is not of an anthracosaurian type, but in this material, juxtaposition is no guarantee of association, and the vertebrae might perhaps belong to the anthracosaurian termed *Calligenethlon* (Steen, 1934, pp. 484-486, figs. 18, 19, 20 B, pl. 2, fig. 1). To add to the confusion, it is quite possible that these animals trapped in hollow stumps may be immature and hence incompletely ossified; a "grown-up" *Calligenethlon*, for example, may have been a true embolomere. On somewhat safer grounds may be the materials described from the Pennsylvanian of Nýřany by Fritsch (1889, pp. 11-13, pls. 50, 52, 53; cf. Steen, 1938, p. 239) as *Diplovertebron*[1] (although even here possible conditions of immaturity cannot be ruled out). In *Diplovertebron* the vertebrae, as seen in side view, appear to be those of an embolomere, with both intercentrum and true centrum parallel-sided structures extending full height to the neural arch base. In end view, however, the intercentrum is incomplete dorsally; the embolomere condition is not attained.

This stage, albeit imperfectly known at present, seems clearly defined and should be named. A name derived directly from *Diplovertebron* might be confusing (as well as lengthy); Diplomeri (by analogy with Embolomeri) may be utilized as a subordinal term for this stage, with *Diplovertebron* used, provisionally, as a type genus until a more ancient, more truly ancestral type be described.

Unless the evolution of a ring centrum occurred more than once, in parallel fashion, among early anthracosaurs, the Diplomeri were a group from which not merely embolomeres but seymouriamorphs and typical reptiles have been derived.[2] The pattern of evolution beyond the diplomerous stage may have been complex. Whether or not the Seymouriamorpha are to be considered reptiles or amphibians remains a moot point. In this group the Discosauriscidae, as Špinar (1952) has shown, have a gilled larva; but it is not impossible that amniote patterns of development may have already been present in the early embryonic stages of such a form. In the partially reduced intercentra, the Seymouriamorpha show a stage of vertebral evolution to be expected in reptile ancestors; but the broadly-developed otic notch of typical seymouriamorphs shows a development hardly to be expected in reptilian ancestors. Possibly we have, in such animals as *Gephyrostegos*, a line paralleling the seymouriamorphs and leading more directly to later reptile groups. I trust that work on Pennsylvanian faunas undertaken by Drs. James and Margaret Brough and others will shed light on this important area. It is, however, beyond the proper limits of the present discussion. I shall at the moment follow this classification:

---

[1] Drs. James and Margaret Brough inform me that certain materials sometimes assigned to this genus (as well as those of *Solenodonsaurus*) are properly to be assigned to *Gephyrostegos*.

[2] I hope to return at a later date, after a description of the cranial structure of the microsaur *Pantylus*, to a discussion (*contra*) of the hypothesis that part, at least, of the reptiles were derived from lepospondyls.

- Order (or Superorder) Anthracosauria
    - Suborder (or Order) Schizomeri. Centrum formed of two discrete half-rings; intercentrum very large, but not complete dorsally. Typical incised otic notch, cheek loosely articulated with skull table. No coracoid ossification. Ilium primitive, as in embolomeres.
    - Suborder (or Order) Diplomeri. Centrum a complete ring; intercentrum large, but not complete dorsally. Otic notch primitive. No coracoid ossification. Ilium as in embolomeres.
    - Suborder (or Order) Embolomeri. Both centrum and intercentrum complete rings. Otic notch primitive. No coracoid ossification. Ilium persistently primitive.
    - ?Suborder (or Order) Seymouriamorpha. Centrum complete, but ossified intercentrum, while persistently large, not extending upward to neural arch. Cheek and table fused, otic notch highly developed. Ascending and posterior processes of ilium joined to form an iliac blade. Separate coracoid ossification.

In the discussion above I have made no mention of amphibian groups, recent or fossil, other than the Labyrinthodontia. It has generally been considered that the Anura are related in some fashion to the Labyrinthodontia, and Watson (1940) advocated descent from *Amphibamus* of the Pennsylvanian, a form obviously related to the rhachitomes. It was on this account that

I erected, in 1947, a subclass Apsidospondyli to include labyrinthodonts and frogs. Subsequent work by Gregory (1950) appears to show that *Amphibamus* is actually a rhachitome, but the possibility of this does not exclude a rhachitomous origin for the Anura. In a recent paper, however, Parsons and Williams (1963) point out various features possessed in common by frogs and urodeles and suggest a common origin for the two groups. If this proves to be the case, the labyrinthodonts will have no descendants except the reptiles, and the term Apsidospondyli is perhaps redundant.

Although I fail to be convinced by Jarvik's arguments for a separate origin of urodeles from fishes (Romer, 1962; cf. Thomson, 1962), the fact that we find throughout the Carboniferous and early Permian varied series of small, non-labyrinthodont amphibians, which I have classed as lepospondyls in a broad use of that term, presents an evolutionary problem for which we have at present no solution. As Watson (1929) notes, amphibians of this sort, already highly specialized, are present in the Lower Carboniferous, at a far earlier age than any labyrinthodonts except the ichthyostegalians. Neither in their spool-shaped holospondylous vertebrae nor in known skull structures do they show the slightest indication of relationship to Labyrinthodontia. It is hoped that restudy of the oldest, Scottish, types will yield further light on their structure. But even so, we will still be confronted here with a major problem in early tetrapod evolution.

REFERENCES CITED

BAIRD, D.

1957. Rhachitomous vertebrae in the loxommid amphibian *Megalocephalus*. Bull. Geol. Soc. Amer., **68:** 1698.

CREDNER, H.

1893. Die Stegocephalen und Saurier aus dem Rothliegenden des Plauen'schen Grundes bei Dresden. X. Theil. Zeitschr. deutsch. geol. Ges., **45:** 639-704.

EATON, T. H., JR. and P. L. STEWART

1960. A new order of fishlike Amphibia from the Pennsylvanian of Kansas. Univ. Kansas Publ., Mus. Nat. Hist., **12:** 217-240.

FRITSCH, A.

1889. Fauna der Gaskohle und der Kalksteine der Permformation Böhmens. Prague, **2:** 1-114.

GREGORY, J. T.

1950. Tetrapods of the Pennsylvanian nodules from Mazon Creek, Illinois. Amer. Jour. Sci., **248:** 833-873.

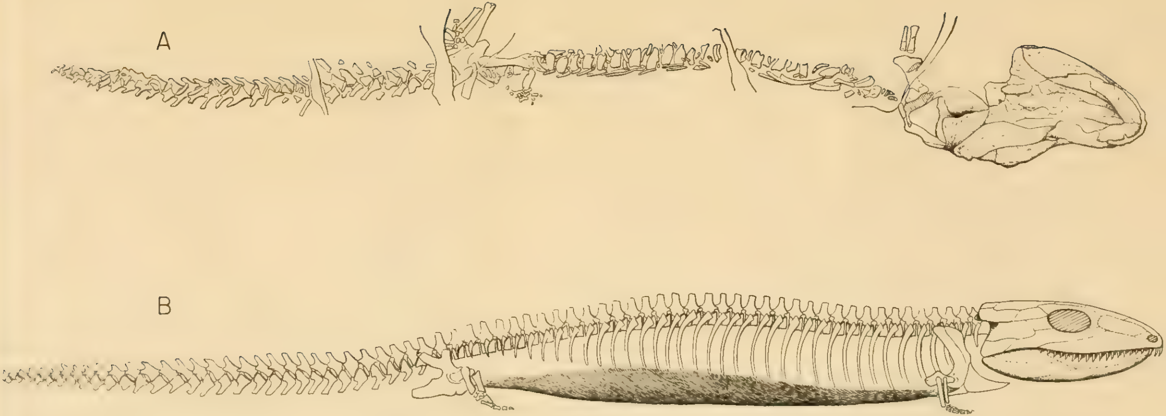


Plate I. *A*, the type specimen of *Pholidogaster pisciformis*, × ¼. Squamation omitted. *B*, attempted restoration, × ¼. As noted in the text, dorsal neural spines, scapula and manus are unknown, and the ribs are incompletely preserved.

HUXLEY, T. H.
1862. On new labyrinthodonts from the Edinburgh coal-field. Quart. Jour. Geol. Soc. London, **18:** 291-296.

JARVIK, E.
1952. On the fish-like tail in the ichthyostegid stegocephalians. Meddel. om Grønland, **114** (12): 1-90.
1955. The oldest tetrapods and their forerunners. Sci. Monthly, **80:** 141-154.

PANCHEN, A. L. and A. D. WALKER
1960. British Coal Measure labyrinthodont localities. Ann. Mag. Nat. Hist., (13) **3:** 321-332.

PARSONS, T. S. and E. E. WILLIAMS
1963. The relationships of the modern Amphibia: a re-evaluation. Quart. Rev. Biol., **38** (1): 26-53.

ROMER, A. S.
1945. Vertebrate Paleontology. Chicago, 687 pp.
1947. Review of the Labyrinthodontia. Bull. Mus. Comp. Zool., **99:** 1-368.
1962. Vertebrate evolution. (Review.) Copeia, 1962 (1): 223-227.

SÄVE-SÖDERBERGH, G.
1935. On the dermal bones of the head in labyrinthodont stegocephalians and primitive Reptilia. Meddel. om Grønland, **98** (3): 1-211.

ŠPINAR, Z. V.
1952. Revise některých moravských Diskosauriscidû. (Revision of some Moravian Discosauriscidae.) Rozpravy Ústředního Ústavu Geologického, **25:** 1-160.

STEEN, M. C.
1934. The amphibian fauna from the South Joggins, Nova Scotia. Proc. Zool. Soc. London, 1934 (3): 465-504.
1938. On the fossil Amphibia from the Gas Coal of Nýřany and other deposits in Czechoslovakia. Proc. Zool. Soc. London, (B) **108:** 205-283.

THOMSON, K. S.
1962. Rhipidistian classification in relation to the origin of the tetrapods. Breviora, Mus. Comp. Zool., **177:** 1-12.

WATSON, D. M. S.
1914. On a femur of reptilian type from the Lower Carboniferous of Scotland. Geol. Mag., (6) **1:** 347-348.
1926. Evolution and origin of the Amphibia. Philos. Trans. Roy. Soc. London, **214:** 189-257.
1929. The Carboniferous Amphibia of Scotland. Pal. Hungarica, **1:** 219-252.
1940. The origin of frogs. Trans. Roy. Soc. Edinburgh, **60** (1): 195-231.

(Received October 14, 1963)

Bulletin of the Museum of Comparative Zoology

HARVARD UNIVERSITY

Vol. 131, No. 7

EARLY EVOLUTION OF THE DISSOROPHID AMPHIBIANS

By Robert L. Carroll

With Two Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
June 30, 1964

PUBLICATIONS ISSUED BY OR IN CONNECTION WITH THE

MUSEUM OF COMPARATIVE ZOOLOGY

HARVARD UNIVERSITY

BULLETIN (octavo) 1863 — The current volume is Vol. 131.

BREVIORA (octavo) 1952 — No. 204 is current.

MEMOIRS (quarto) 1864–1938 — Publication terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 41 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 28 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained from the Publications Office of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Peters' Check-List of Birds of the World. Volumes 1, 4 and 6 are out of print; volumes 2, 3, 5, 7, 9, 10 and 15 are currently available.

Phylogeny and Evolution of Crustacea. Proceedings of a conference held at Cambridge, Mass., March 6-8, 1962. H. B. Whittington and W. D. I. Rolfe, editors. Cambridge, Mass., 192 pp., 80 figs., 1963. Cloth bound, $6.75.

Fishes of the Gulf of Maine, by Henry B. Bigelow and William C. Schroeder. Washington, viii - 577 pp., 1953. Photo-offset reprint, $6.50.

PUBLICATIONS OF THE BOSTON SOCIETY OF NATURAL HISTORY

The remaining stock of the scientific periodicals of the Boston Society of Natural History has been transferred to the Museum of Comparative Zoology for distribution. Prices for individual numbers may be had upon request.

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 7

EARLY EVOLUTION OF THE DISSOROPHID AMPHIBIANS

By Robert L. Carroll

With Two Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
June, 1964

Bull. Mus. Comp. Zool., Harvard Univ., 131(7): 161-250, June, 1964.

No. 7 — *Early Evolution of the Dissorophid Amphibians*[1]

By Robert L. Carroll[2]

TABLE OF CONTENTS

Introduction 163

Morphology of *Tersomius* 165
- Material Studied 166
- General Features of the Skull 168
- Separate Skull Elements 173
- Postcranial Skeleton 192

Other Early Permian Dissorophids 192
- *Broiliellus* 195
- *Dissorophus* 202
- *Brevidorsum* 210
- *Aspidosaurus* 214
- *Conjunctio* 218
- Interrelationships of the Permian Dissorophids 223

Pennsylvanian Dissorophids 227
- *Amphibamus lyelli* 227
- *Amphibamus calliprepes* 241
- *Amphibamus grandiceps* 242
- *Arkanserpeton arcuatum* 244
- Interrelationships of the Pennsylvanian Dissorophids . . 244

Relationships of the Dissorophidae among the Rhachitomi 245

Literature Cited 248

INTRODUCTION

The general phylogeny of the rhachitomous amphibians has been outlined in Romer's Review of the Labyrinthodontia (1947). The detailed evolutionary pattern of most of the families in this group, however, has yet to be determined. In many of the families the fossil record is still too incomplete to give a coherent picture. The deposits of the Lower Permian of Texas,

---

[1] Published by a grant from the Wetmore Colles Fund.

[2] A draft of this paper was submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Harvard University.

however, have accumulated over a sufficient length of time to record adequately the histories of several groups; one of these is the family Dissorophidae. This family has always attracted interest because its members possess a variety of patterns of dermal armor. The armor is in the form of single or double rows of plates resting above the vertebral column, in some genera forming a carapace resembling that of turtles. Dissorophids are further typified by the presence of a prominent pattern of cranial ridges and by conspicuous otic notches, closed posteriorly in some genera. All of the genera which have been described are relatively small, reaching a total length of a foot or so.

Differences in the armor have made possible a much more detailed classification of this group than could be made from a study of other skeletal features; for this reason, the family has been divided into a larger number of genera than has any other family of rhachitomous amphibians. The classification of these genera has been subject to a number of interpretations, most recently reviewed by DeMar (unpublished thesis, University of Chicago).

Most of the genera which have been described come from the Clear Fork group, by which time the various patterns of armor had become fully differentiated. In addition, there are a large number of specimens from the earlier, Wichita group. These specimens enable us to trace the early evolution of the armored dissorophids, and to determine their affiliation with several members of the family which have been described from the Pennsylvanian.

Much of the material in the Harvard collection belongs to the genus *Tersomius*, described by Case in 1910, and included as a primitive member of the Dissorophidae by Romer in 1947. Since this genus is so well represented, it will be described in detail as a basis for determining relationships among the other members of the family. This description forms the first part of this paper. In the second part, several new species of Permian dissorophids are described, together with a discussion of the general pattern of evolution within the family during that period. The Pennsylvanian dissorophids are discussed in the last section.

I wish to express my appreciation to Dr. Romer for suggesting this study and for offering many helpful suggestions throughout the course of the work. I would also like to thank Dr. Baird, at Princeton, who graciously allowed me to describe several specimens from Linton, Ohio, which he had prepared, and Dr. Dalquest at Midwestern University, Wichita Falls, Texas, for two specimens of *Tersomius* which he gave to the Museum of Comparative Zoology. For information concerning the Clear Fork dissorophids, and particularly their armor, I am grateful to Dr. DeMar at the University of Chicago, and I wish to thank him for permission to summarize his findings. Yale Peabody Museum and the American Museum of Natural History have been very helpful in loaning material. I would also like to thank Professor Patterson and Dr. Williams for critical reading of the manuscript.

MORPHOLOGY OF *TERSOMIUS*

TERSOMIUS Case 1910

Type species. Tersomius texensis Case 1910.

New diagnosis: Primitive dissorophid, lacking cranial ornamentation. Otic notch not closed posteriorly. Frontal bone entering margin of orbit. Each jaw has 45-50 teeth. Internarial bone present.

TERSOMIUS TEXENSIS Case 1910

Figures 1-8

Tersomius texensis Case, 1910, p. 180.

Type: AMNH[1] 4719. Small skull with lower jaws. Left nasal region and the very back of the skull are missing and the palate is not exposed. Both orbits show remains of superficial eye plates. A second, fragmentary skull accompanies the type. It includes only the back portion of the left side, and apparently it was overlooked by Case in his original and subsequent (1911) descriptions because of its small size. A tibia and humerus were collected with these skulls, but their size precludes association.

Locality: South side of Little Wichita River, Archer County, Texas.

Horizon: Belle Plains Formation, Wichita group, Lower Permian.[2]

Diagnosis: Same as for genus. This is the only species known.

---

[1] Museum abbreviations: AMNH, American Museum of Natural History; BM(NH), British Museum (Natural History); CNHM, Chicago Natural History Museum; MCZ, Museum of Comparative Zoology; UCMP, University of California Museum of Paleontology; USNM, United States National Museum; YPM, Yale Peabody Museum.

[2] A correlation chart of Permian and Pennsylvanian stratigraphy follows the text. Correlation of Texas localities is based on Romer, 1958.

MATERIAL STUDIED

Since Case's original description, a great deal more material of this species has been discovered. Because there may be some variation from one formation to another, the material from each formation is listed separately.

Belle Plains Formation

MCZ 3351 and 3352. Two skulls with lower jaws, impregnated with ironstone and slightly distorted. Collected by Dalquest three miles east of Wichita Falls, Texas, E. Morrison survey, abstract no. 186.

Putnam Formation, Archer City bone bed

MCZ 1912 (Fig. 2). Skull and lower jaws, compressed longitudinally but otherwise undistorted, except for crushing of the rear portion of the braincase, occipital region and rear part of the parasphenoid. Collected by N. E. Wright, 1948, one mile southwest of Archer City, Texas; prepared by S. J. Olsen. The description of the palate and skull roof is based on this specimen.

MCZ 1415 (Fig. 1A). Skull and lower jaws, complete except for surface of bones in front of orbits, with very little distortion. This skull is the basis for the description of the parasphenoid, occipital region and lower jaw. Collected by R. V. Witter and party, 1936.

MCZ 1696. Jaw fragments collected by Witter and party, 1936.

MCZ 1694 (Fig. 1B). a. Skull behind orbits, probably collected by Witter and party, 1936. Sectioned transversely at ½ millimeter intervals employing the cellulose acetate peel technique. Basis of descriptions of otic and occipital regions.

b. Back of left ramus of lower jaw and fragment of cheek region. Possibly associated with previous specimen.

MCZ 3237. Skull in front of orbits with lower jaws in place. Collected with MCZ 1694. Removal of skull roof from this fragment allowed investigation of the dorsal surface of the palate.

MCZ 3236. Skull in front of orbits, sectioned transversely at ½ millimeter intervals. Collected with MCZ 1694. Basis of nasal region description.

MCZ 3235. Skull in front of orbits with lower jaws. Collected with MCZ 1694. Furnished portions of inner surface of lower jaws not seen in MCZ 1415 or 1694.

MCZ 3234. Front of braincase between orbits, sectioned transversely at ½ millimeter intervals. Found in either 1939 or

1941. Basis for description of the anterior region of the braincase.

Pueblo-Moran boundary

MCZ 1911 (Fig. 1D). Nearly complete skull and lower jaws. Right side of skull turned under palate. Palate badly distorted, left side of skull flattened, back of skull entirely gone. Collected by N. E. Wright, 1948. It was found north of the west fork of the Trinity River, section 1834, Texan Emigration and Land Co., Archer County, Texas.

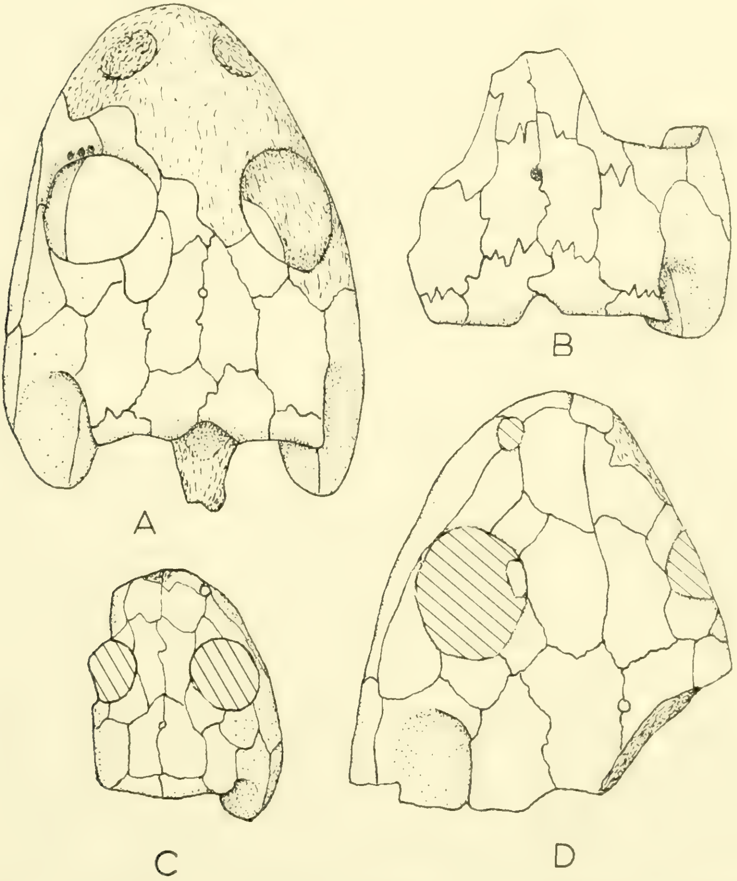


FIG. 1. Skulls of *Tersomius*. A, MCZ 1415; B, MCZ 1694; C, AMNH 4719; D, MCZ 1911. × 1.

Skulls utilized for description: The following description is based entirely on the Archer City specimens. Because of the small size and incomplete nature of the type skull, it cannot be stated categorically that it belongs to the same species as do the other specimens, although there is nothing to differentiate them in the material at hand. In contrast to Case's drawing, the prefrontal and postfrontal do not meet over the orbit. In general outline, the other Belle Plains specimens, collected by Dalquest, are indistinguishable from those from Archer City. The matrix has been partially removed from them, but ironstone has destroyed the surface of the bone by infiltration, making detailed investigation impossible. Some features suggest that the geologically oldest skull, MCZ 1911, may differ slightly from the Archer City skulls; its peculiarities will be discussed in the second section. Neither this specimen nor the type is relied upon for this description.

Because of the small size and fragile nature of the skulls, it was impossible to clean the inside surface of many of the cranial bones. For this reason it was necessary to section virtually the entire skull. Cellulose acetate peels were made from three large fragments of different animals. These peels were stained in a one per cent solution of aniline blue in water. This stained the bone a deep blue and the matrix remained its natural color.

Unfortunately, not all of the specimens are of the same size or even relative dimensions. For this reason composite reconstructions of the under surface of the skull roof, the braincase, and the upper surface of the palate cannot correspond exactly with the dimensions of the surfaces taken from a whole specimen. Drawings were made from enlarged photographs of the whole specimens and from projections of the serial sections.

General Features of the Skull

Evidently the type specimen was an immature animal when it died, since its sutures are open. Although the type and accompanying skull have almost identical dimensions, the latter has closed sutures. Presumably this indicates that these sutures close quite rapidly once the animal has reached a certain age. The estimated length of the type skull is about 60 per cent of that of MCZ 1912. Probably MCZ 1912 and the other Archer City specimens are mature since all fall within about 10 per cent of a median size. The fragments are all of specimens slightly smaller than the complete skulls.

Although much of the information regarding the skull roof and palate is taken from MCZ 1912 (Fig. 2), a better idea of the relative dimensions is gained from MCZ 1415 (Fig. 1A). The roof bones in front of the orbits are mostly destroyed, but the marginal bones and the lower jaws are intact, preserving the outline of the skull. There appears to be very little distortion.

The skull is small — only 64 mm from the tip of the snout to the end of the quadrates — and narrow, 47 mm at the widest point just behind the orbits. The highest point on the skull is at the rear of the skull table, 15 mm above the base of the quadratojugal. The relative dimensions of height, width and length are quite similar to those of *Eryops* (Sawin, 1941), but the positions of the orbits, otic notch and external nares are not. The orbits are proportionately large, extending laterally to within a millimeter or two of the edge of the skull, and medially to the frontal bones. They are located slightly anterior to the middle of the skull. The external nares are 6 mm in diameter and are located near the margin of the skull, less than 3 mm from its end. Their separation is equal to that of the orbits, about 10 mm. The septomaxillae cover the posterior portion of the nares. Because of the curvature of the skull, both the orbits and the external nares look out and forward.

As in *Eryops*, the quadrates extend beyond the back of the skull roof. Viewed dorsally, the skull table occupies most of the width of the skull, but is separated from the jaw suspensorium by a deep otic notch, incised 13 mm from the end of the tabular. The side margins of the skull form a continuous arc from the tip of the quadrate to the end of the snout. The skull table behind the orbits is almost flat. In front of the orbits the roof slopes in a convex curve to the tip of the skull. In front of the otic notch the sides of the skull slope down at about a 45° angle. The posterior margin of the skull table is horizontal or slightly depressed above the foramen magnum. The posterior, unsculptured portion of the postparietals and tabulars slopes at about a 45° angle toward the occipital condyles. The lateral posterior surface of the tabulars is sculptured and extends posteriorly beyond the level of the sculptured portion of the postparietals.

Specimen 1912 has large bony plates extending over the orbital cavity and projecting 6 mm above the skull roof. They are connected to the rear and medial portions of the orbital margin and evidently served to protect the eye. Apparently they were composed of one solid piece of bone since there is no consistency between the fracture patterns of the two eye plates. The plates are sculptured in the same manner as the remainder of the cranial bones. Remnants of eye plates were also seen in MCZ 3234, AMNH 4719, and MCZ 1911. The Pennsylvanian dissorophid *Amphibamus* had similar eye plates, both in the Linton species *lyelli* and the Mazon Creek species *grandiceps*.

The pineal opening is much further forward in *Tersomius* than in *Eryops*. The ratio of its distance from the foramen magnum to the total skull length is 1:3.5, compared with a 1:9.3 ratio in *Eryops* (Romer and Edinger, 1942). It is a millimeter or so in diameter, and is located just behind a line joining the posterior margins of the orbits.

With one exception, the roofing bones are those usually encountered in an advanced rhachitomous form. The exception is an internarial bone located between the premaxillae and the nasals, in the same position as a bone in the ichthyostegids and some loxommids.

No ridges, rims or hollows are present on the roof. The individual bones are covered with a uniform fine pitting. This pitting does not extend into the otic notch. Presumably the place at which the sculpturing stops marks the position of the tympanic membrane. The occipital surface of the postparietals and tabulars also lacks sculpturing. There are no areas which could be considered as regions of secondary growth in the sense of Bystrow (1935).

A ventral view of the skull (Fig. 4A) shows very large interpterygoid vacuities bordered laterally by narrow palatal bones. In addition to marginal teeth on the maxillae and premaxillae, there are tusk-pairs on the ectopterygoid and palatine bones and two tusk-pairs on each vomer. Very fine denticles are present on all the bones except the parasphenoid. These are most conspicuous on the pterygoid.

The parasphenoid and rear part of the pterygoids are best seen on MCZ 1415. The posterior plate of the parasphenoid is quite wide and underlies the back of the braincase. Basipterygoid processes extend laterally behind the articulating rami of the pterygoids, one-fourth of the distance from the back of the skull, to form the basicranial articulation. The cultriform process continues forward beneath the braincase to reach the vomers, dividing the interpterygoid vacuities medially.

The internal nares are proportionately rather large. Between them, just behind the front of the skull, lies a depression about the same size as an internal naris, termed the internarial pit, formed by the bending of the vomers toward the skull roof. The posterior halves of the adductor fenestrae are expanded medially for the temporal musculature.

The margin of the palate is in a single plane. As viewed from *below*, the vomers are depressed medially for the reception of the parasphenoid as well as for the pit in front. The posterior portion of the pterygoid rises above the remainder of the palate as it surrounds the median portion of the adductor fenestra. The parasphenoid is slightly depressed below the margin of the palate. The maxilla and premaxilla rise a millimeter or two above the lateral margin of the palatine bones, and overlap them to a variable extent. The articular surface of the quadrate

TABLE 1

Cranial Dimensions of *Tersomius*

	Type AMNH 4719	MCZ[1] 1912	MCZ 1415	MCZ 1694	MCZ 3234	MCZ 1911
Length of cranium to extremity of quadrate	34	58	64	—	—	—
Length of cranium to foramen magnum	32	52	58	—	—	—
Depth of skull in front of otic notch	9	14	15	13	—	14
Greatest width of cranium between quadratojugals	36	58	47	51	—	62
Least width of skull table dorsal to otic notch	22	33	33	32	—	34
Least width between orbits	7	11	10	11	10	14
Transverse diameter of orbits	11	17	14	14	—	18
Longitudinal diameter of orbits	11	15	17	—	—	16
Distance from center of orbit to quadrate	19	36	38	35	—	—
Distance from center of orbit to front of skull	15	24	26	—	—	28
Distance of pineal from back of skull roof	10	18	21	25	—	—
Back of orbit to front of otic notch	7	13	13	12	—	11

[1] Specimen compressed longitudinally.
Dimensions of specimens are to the nearest millimeter.
Measurements taken from projections onto a flat surface.

extends ventrally slightly beyond the margins of the pterygoid and quadratojugal.

The upper surface of the palate (Fig. 5B) reflects, by and large, its lower surface. Above the vomers, however, are ridges projecting dorsally a millimeter or more, bordering the medial margins of the internal nares. These ridges extend back onto the palatines. Where the vomers meet above the internarial pit, they extend to the roof of the skull, separating the nasal sacs.

The underside of the skull roof (Fig. 4 B) conforms to the contours of its external surface except in the region of the snout and front of the braincase. The depressions for cartilaginous nasal capsules are the most prominent feature. They extend from the external nares posteriorly to the front of the orbits. Medially they are bordered by a ridge on the nasal and prefrontal bones. Laterally they terminate at the juncture of the skull roof and palate. A passage for the nasolacrimal duct traverses the roof of the depression for the nasal sac. The passage is in the form of an open groove from the lip of the external naris to the middle of the depression, at which point it becomes enclosed in the bone of the lacrimal and continues as a raised tube to the front of the orbit, where it passes through three small holes in the edge of the lacrimal bone.

Medial to the ridge on the nasal bone there is a groove which runs from the nasal-prefrontal boundary to the mid-point of the ridge. At this point the center of the skull between the nasal sac depressions is flat. The olfactory nerve may have crossed into the nasal sac where the medial groove terminates. Immediately lateral to this ridge, in fact partially enclosed in its lateral edge, is a groove or tube which probably helped to secure the margin of the cartilage of the nasal capsule.

The occipital region (Fig. 5 A) was somewhat weathered in MCZ 1415, but the sectioned material serves to reconstruct the area. The double condyle is formed by the exoccipitals which reach dorsally on either side of the foramen magnum. The postparietals extend ventrally to border this opening. Below the foramen magnum is a slit above the medial juncture of the exoccipitals. This may have been filled with the otherwise missing basioccipital and, as Sawin suggests in *Eryops,* the forward projection of the notochord. Lateral to the exoccipitals are the otic bones; paroccipital processes from these bones extend laterally and dorsally to the tabulars, bounding the posttemporal fossae ventrally. These openings are bordered dorsally by the bones of the skull roof.

The anterior portion of the braincase is visible between the interpterygoid vacuities. The sphenethmoid bones run the length of the palate between the parasphenoid and the skull roof. The posterior part of the braincase is mostly concealed by the parasphenoid, except for the exoccipitals and otic bones which are visible posteriorly.

The mandible (Fig. 8) extends the full length of the skull. It differs from that of *Eryops* in being much shallower in the region of the angular. Posteriorly the lower margin ascends gradually to the articular. Anteriorly the jaw tapers slightly, a feature accentuated in articulated specimens by the tendency of the jaws to be bent underneath the forepart of the skull. The coronoid process extends slightly higher above the tooth row in *Tersomius* than in *Eryops*. Forty-seven teeth are carried on the dorsal surface of the dentary, and there are two more large teeth on the lower inside surface of that bone, lateral to the symphysis. There is no trace of coronoid teeth. On the medial surface of the jaw there is a large meckelian fossa below the coronoid process, a smaller inframeckelian fossa and a tiny mandibular foramen. No trace of dental or mental foramina was seen. The lateral surface of the jaw is sculptured like the bones of the skull roof. One peculiarity of this genus is the presence of quite large fragments of bone lying between the rami (Fig. 3). They extend from the symphysis approximately halfway to the rear of the jaw and are found with even the small fragments of the snout. They have not been observed in any other dissorophids. These fragments are pitted in the same manner as are the lateral jaw surfaces and the roof of the skull.

SEPARATE SKULL ELEMENTS

Dermal bones of the skull roof: Due to the size and position of the orbits and otic notches, the skull of *Tersomius* differs markedly from such a "typical" rhachitome as *Eryops*. Hence it is of value to describe the position and configuration of each element.

The flat portion of the skull table is composed of six paired units: frontals, postfrontals, parietals, postparietals, supratemporals and tabulars. The tabulars are small bones making up the posterolateral edge of the skull table. They extend back over the occipital region medially, where they are unsculptured.

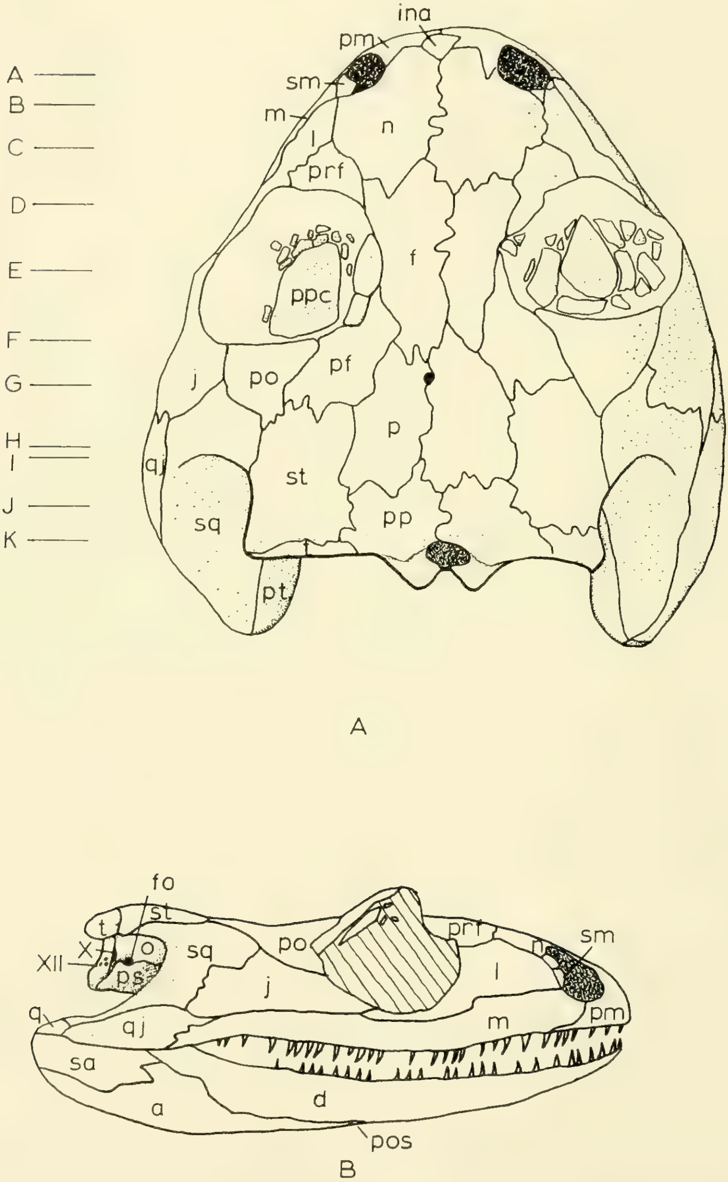

ina
pm
sm
m
l
n
prf
ppc
f
pf
po
j
p
st
qj
sq
pp
pt
A
B
C
D
E
F
G
H
I
J
K
A
fo
st
t
X
XII
o
ps
sq
po
prf
n
sm
l
j
q
qj
m
pm
sa
a
d
pos
B

FIG. 2. *Tersomius texensis.* A, Dorsal view of skull, MCZ 1912 (Letters A-K refer to sections shown in Figure 6); B, Lateral view of skull, MCZ 1912. × 1⅓. List of abbreviations follows text.

Ventrally they send projections medially to the paroccipital processes of the otic bones. Medial to the tabulars are the postparietals. They extend twice as far forward on the skull roof as do the tabulars and, as is the case in other temnospondyls, are broadly in contact with the supratemporals. Unsculptured ventral flanges of the postparietals extend onto the occipital region on either side of the foramen magnum. In front of the tabulars are the supratemporals; they are among the largest skull units. The lateral margin of the supratemporal borders the squamosal above the otic notch. Posterior to the squamosal, the supratemporal itself borders the notch, at which point its margin is unsculptured. Anteriorly the supratemporal reaches the circumorbital bones. Medial to the supratemporals and anterior to the postparietals are the parietals, between which is the pineal foramen. This opening narrows from the lower to the upper surface of the bones. In front of the parietals are the large frontals. They extend to the margins of the orbits and support a portion of the bony eye plates. Anterior to the supratemporal bones, and lateral to the parietals and frontals, are the postfrontals which also border the orbits and support part of the eye plates.

Bordering the skull table are the bones of the lateral skull wall. The squamosal surrounds much of the otic notch. Its contact with the supratemporal occurs along the dorsal margin of the notch. The otic notch slopes ventrally from just beneath the skull roof toward the quadrate, and is floored by the squamosal, quadratojugal and pterygoid. The squamosal meets the pterygoid medially. The lateral margin of the squamosal is in contact with the jugal and quadratojugal. The latter bone extends medially in the posterior portion of the notch floor to reach the pterygoid. The quadrate underlies these two bones at this point and extends only slightly further to the rear than they do. On the under surface of the skull roof the squamosal sends a large flange of bone parallel to the pterygoid along their juncture, beneath the anterior margin of the otic notch. This extension is not directly articulated to the pterygoid, but apparently helped strengthen the union of the two bones. Sawin suggests a cartilaginous connection from this flange, in *Eryops*, which would associate this structure with the palatoquadrate arch.

In front of the otic notch are the circumorbital bones. The postorbital extends from the skull roof down over the cheek region. It shares with the frontal and postfrontal the task of supporting the palpebral cup. The jugals extend beneath the orbits, lateral to the postorbitals, to the lacrimals. The lateral margins of the jugal and lacrimal as well as the maxilla are partially obscured in dorsal view by the ventral inturning of the skull margin. The jugal does not extend toward the skull margin across the maxilla as it does in *Broiliellus.* The jugal and lacrimal extend medially and ventrally beneath the orbit to reach the palate. Each sends a flange inward from the externally visible dorsal surface (best seen in transverse sections D and E, Fig. 6). Nothing of this nature occurs in *Eryops*, whose orbits are high above the palate. The lacrimal and prefrontal continue this medial extension in front of the orbit. Three holes in the lacrimal bone open into the lacrimal duct. The lacrimal bone extends medially beneath the internal nares, providing a lateral floor for the nasal capsule. At this point it is below the surface of the medial margin of the internal nares.

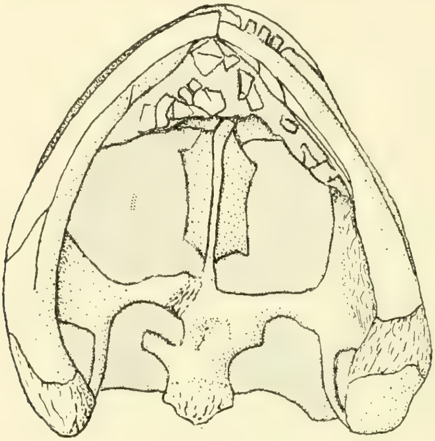


FIG. 3. *Tersomius texensis.* Palatal view of MCZ 1912 showing dermal ossifications between lower jaws. × 1.

Between the lacrimal bone and the external naris is the septomaxilla. This bone extends into the external naris halfway to its front margin. It articulates with the lacrimal, maxilla, premaxilla and vomer. The nasal, maxilla and premaxilla form the balance of the margin of the external naris. The internasal is a small diamond-shaped bone between the nasals and premaxillae. It is located at the juncture of the vomers and the skull roof. Its position is the same as that of the medial rostral fontanel in *Parioxys*, the trematopsids, and the zatrachyids. In MCZ 3235, the bone is missing, indicating the possibility of confusing a foramen with the mere loss of the bone. No particular function is suggested for such a bone, but it might be noted that the skull roof becomes superfluous where the vomers and premaxillae are in contact with the surrounding skull roof units.

The premaxillae and maxillae meet beneath the hind part of the external nares. Together, they bear a uniform assemblage of marginal teeth, each tooth a simple peg, slanting slightly posteriorly. Room for 34 teeth in the maxilla and 13 in the premaxilla corresponds exactly with the number of teeth in the lower jaw. No particular pattern of tooth succession was noted. The teeth are the same size throughout the jaw. Where they are complete they reach a length of approximately 2 mm. The remainder of the skull margin is composed of the quadratojugal, which meets the maxilla below the otic notch, and the quadrate.

Completing the skull roof are the nasal bones. They have one of the largest surface exposures of the dorsal units. They extend from the frontals to the premaxillae; laterally they reach the prefrontals and the lacrimals. Their ventral elaboration in connection with the nasal sacs has already been pointed out.

Dermal bones of the palate: The palate is composed of the paired pterygoids, ectopterygoids, palatines and vomers, the median parasphenoid, and the medial extensions of the maxillae and premaxillae. The pterygoid is one of the most complicated bones in the skull. It consists of (1) a median basipterygoid region which articulates with the parasphenoid and basisphenoid, (2) a quadrate ramus extending almost vertically toward the squamosal and supratemporal, and posteriorly to the quadrate, and (3) a palatine ramus extending forward to the ectopterygoid and palatine bones.

The basipterygoid region forms a firm connection with the medial portion of the skull. A broad connection is made between a ventrally directed flange of the parasphenoid and the pterygoid. This is reinforced by the basisphenoid which overlaps both bones at this point. Although it is clear that such an arrangement is intermediate between that observed in an animal with a movable palate and the type of sutural connection present in *Eryops*, it is doubtful that any movement was possible in

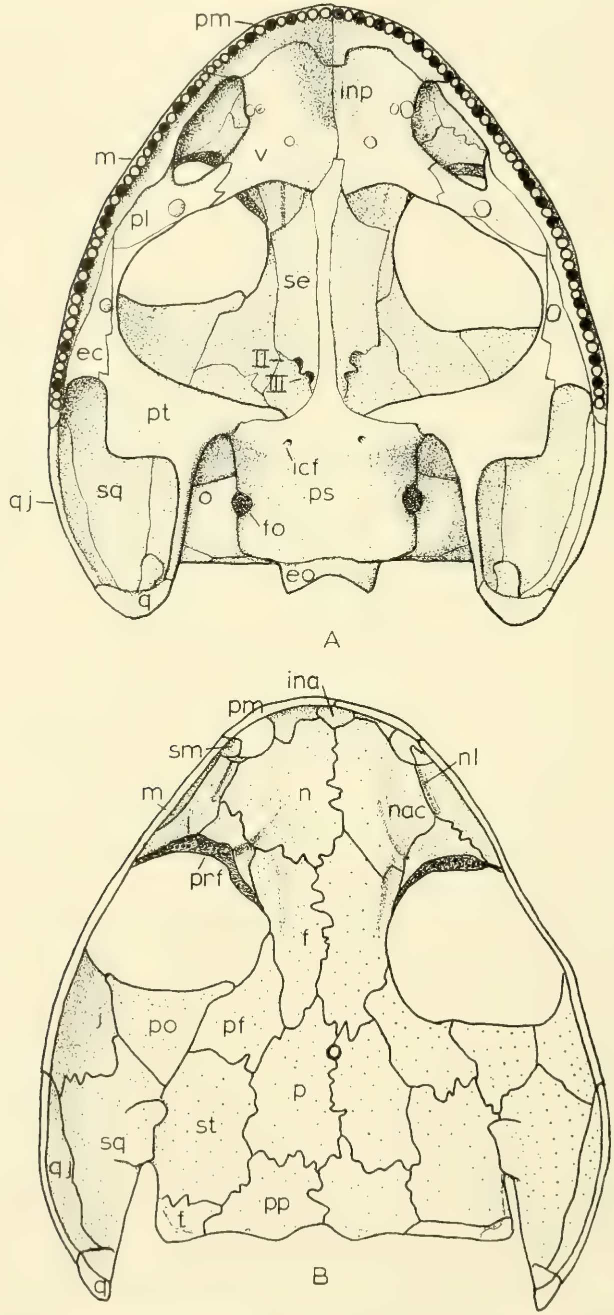

pm
inp
m
v
pl
se
ec
II
III
pt
icf
qj
sq
ps
o
fo
eo
q
A
ina
pm
sm
nl
m
n
nac
l
prf
f
j
po
pf
p
st
sq
qj
pp
t
q
B

FIG. 4. *Tersomius texensis.* A, Ventral view of palate, MCZ 1912, parasphenoid restored from MCZ 1415; B, Ventral view of skull roof with palate removed, composite drawing. × 1⅓.

this palate. The quadrate ramus extends behind the basipterygoid articulation. Its ventral margin is in the plane of the palate and forms the medial and posterior margins of the adductor fenestra. Dorsally it extends toward the squamosal beneath the otic notch, forming the medial portion of the floor of this structure. The line of contact between the squamosal and pterygoid slopes toward the quadrate at the rear of the skull. Posteriorly, the pterygoid overlaps the quadrate. The palatal ramus extends forward medial to the ectopterygoid and palatine bones. On the specimen examined, it does not reach the vomers. Such a thin strip passes the ectopterygoid and palatine that one might suspect that it had originally been wider, although the specimen shows no definite sign of breakage or irregularity. No dorsal groove for a palatine cartilage was seen.

The ectopterygoid, bearing one large tooth, forms the front margin of the adductor fenestra, and extends anteriorly to the palatine. Its lateral margin is covered ventrally by the maxilla. The palatine bears the same relation to the maxilla as does the ectopterygoid, and also carries one large tooth. It has a narrow dorsal ridge on the posterior margin of the internal naris.

The vomers form the anterior region of the palate. Posteriorly they border the interpterygoid vacuities, and laterally the internal nares. On the margin of the internal naris each bears a dorsal ridge continuous with that of the palatine and formed in the same manner, by an incurling of the margin of the bone, best seen in Figure 6 C. The anteromedial portion of the vomers extends toward the skull roof. In front of the nasal sacs, the right and left vomers part to leave a narrow cleft in the palate which is covered ventrally by the premaxillae. Apparently this configuration of the vomers serves to support the medial portion of the nasal sacs. The internarial pit certainly is much larger than would be necessary to accommodate the parasymphysial tusks. Posteriorly the vomers rise to meet the parasphenoid and sphenethmoid. The vomers each bear two tusk-pairs. One is located at the anterior margin of the internal naris, in a comparable position to the single pair in *Eryops*. The other is located posteriorly and medially, halfway to the juncture of the two vomers. Both tusk-pairs are on the rim of the depression between the internal nares.

The parasphenoid is divisible into an anterior cultriform process and a posterior plate bearing the basipterygoid articulation and underlying the posterior portion of the braincase. The cultriform process extends anteriorly to reach the vomers;

for most of this distance it underlies the sphenethmoid. It extends across the ventral surface of the vomers approaching the posterior vomerine teeth. Behind the basicranial articulation the parasphenoid rises abruptly to a flat platform. Laterally it extends processes that surround the ventral portion of the otic region of the brain. Posteriorly the plate extends to the occipital region, lying just beneath the exoccipitals. Just behind the point of pterygoid articulation, the internal carotid arteries

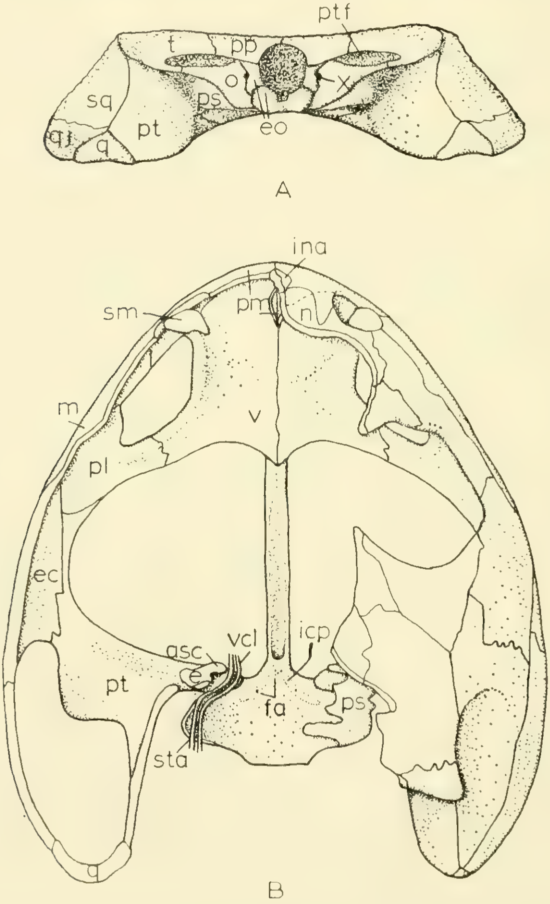


FIG. 5. *Tersomius texensis.* A, Posterior view of skull; B, Dorsal view of palate; dashed line on premaxilla and nasal indicates point at which vomer reaches skull roof. × 1⅓.

enter the parasphenoid. They are not readily apparent in an intact skull, but are revealed in sectioned material. In *Eryops* these arteries cross the lower surface of the parasphenoid and enter the skull anterior to the pterygoid articulation. The dorsal surface of the parasphenoid will be discussed with the braincase.

In addition to carrying the marginal teeth and forming the margin of the skull roof, the maxillae and premaxillae extend ventrally across the margin of the ectopterygoid and palatine bones. The premaxillae do the same beneath the vomers, covering completely the cleft where the vomers approach the skull roof. These are not simply contacts as in *Eryops*, but an overlapping, so that removal of the marginal skull bones reveals bones of the palate above them, as if the palate were resting on a moulding.

The palate of *Tersomius* differs from that of *Eryops* in the following features:

(1) greater size of interpterygoid vacuities
(2) strong contact between parasphenoid and vomers
(3) failure of pterygoid to reach vomers
(4) overlapping, rather than sutural connection between parasphenoid and pterygoid
(5) presence of two vomerine tusk-pairs
(6) passage of internal carotids through parasphenoid behind basicranial articulation
(7) presence of internarial pit.

The primary palatoquadrate arch: The primary palatoquadrate arch is composed of the epipterygoid and the quadrate, remains of the palatoquadrate cartilage.

The quadrate is a solid bone, roughly tetrahedral in shape, which articulates with the articular of the lower jaw. The base of the tetrahedron forms the articulating surface and has a concavity parallel with the long axis of the jaw. The medial portion of the articulating surface extends further anteriorly than does the lateral. The dorsal anterior surface is covered by the squamosal, quadratojugal and pterygoid. Only the posterior surface is exposed when the jaws are closed. The apex of the quadrate extends dorsally above the floor of the otic notch. There is an anterodorsal extension of the quadrate beneath the pterygoid.

The epipterygoid, visible only in the sectioned skull, MCZ 1694, is divided into two parts, an ascending process arising just lateral to the basicranial articulation, and a proötic process, which is disarticulated from the remainder of the epipterygoid in this specimen. The ascending process is a stout rod of laminar bone articulating with the pterygoid at the juncture of the quadrate ramus and the basipterygoid region. It is 7 mm long and reaches within 1 or 2 mm of the skull roof lateral to the braincase (which is unossified in this area), slanting medially about 20° from the vertical. The rod ends abruptly anteriorly, but slopes slightly on its posterior margin. The base of the ascending process is about 2½ mm thick. Posteriorly it articulates with the basisphenoid and the parasphenoid as well as with the pterygoid.

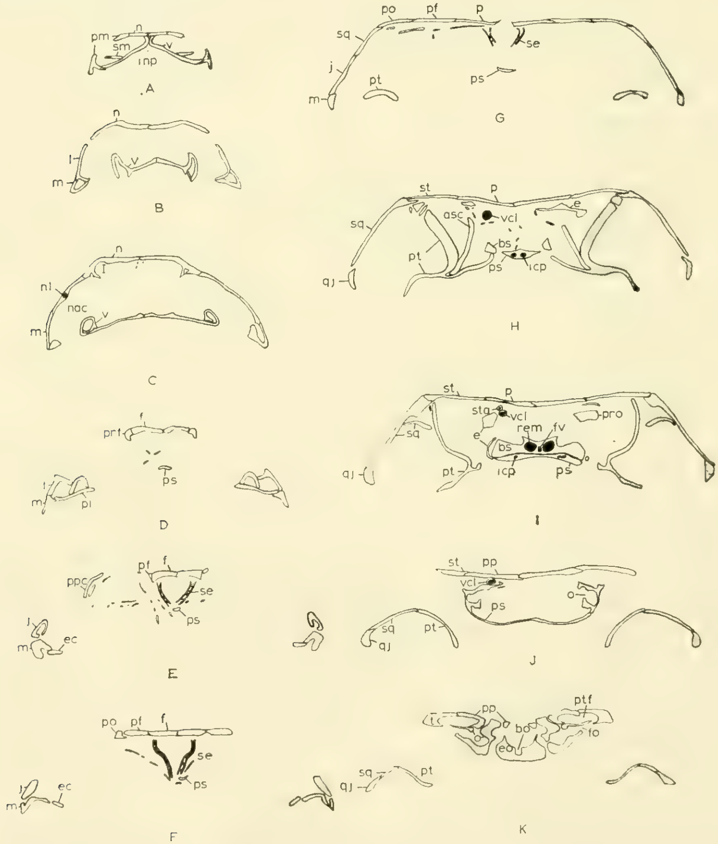

pm
n
sm
v
inp
A
n
l
v
m
B
n
nl
l
nac
v
m
C
prf
f
ps
l
m
pl
D
ppc
pf
f
se
ps
j
m
ec
E
po
pf
f
se
ps
j
m
ec
F
po
pf
p
sq
se
j
pt
ps
m
G
st
p
e
sq
asc
vcl
bs
pt
qj
ps
icp
H
st
p
stg
vcl
pro
sq
e
rem
fv
bs
qj
pt
icp
ps
o
I
st
pp
vcl
ps
o
sq
pt
qj
J
ptf
pp
bo
fo
eo
sq
pt
qj
K

FIG. 6. *Tersomius texensis.* Transverse sections of skull; positions indicated in Fig. 2 A. Sections A-C from MCZ 3236, D-F from MCZ 3234, F-K from MCZ 1694; stippled areas are restored. × 1.

Lateral to the braincase, in the region of the basicranial articulation, there are two bony rods which lie just beneath the skull roof. These do not articulate with any of the other bones of the skull. The right rod is 3½ mm long, and its anterior end lies just posterior to the dorsal extremity of the ascending process of the epipterygoid. The left rod is 5½ mm long and lies mostly anterior to the ascending process (Fig. 6, sections II and I). Although the bars are of unequal length, it is evident that they are paired structures. From the configuration of the epipterygoid in *Dissorophus angustus* (Fig. 13 E) and in several genera discussed by Sushkin (1927), it is evident that these paired structures are the proötic processes of the epipterygoids which have become disarticulated from the remainder of these bones. Judging from *D. angustus*, the left proötic process is probably nearly complete in this specimen of *Tersomius*. The orientation of the bone in the two genera is probably similar, the anterior end articulating with the base of the ascending process, and the remainder of the bone extending dorsally at about a 45° angle from the base of the skull toward the anterior extremity of the otic capsule. Whether it articulated with the otic capsule in *Tersomius* is not known. In *Tersomius* the proötic process is roughly cylindrical anteriorly, but quite flat and wide posteriorly. Unlike the ascending process, the proötic process is composed of very porous bone, giving the appearance of being hollow at its anterior extremity.

There is no real quadrate ramus of the epipterygoid. Because of the deep otic notch, the quadrate ramus of the pterygoid extends far anteriorly and so appears lateral to the ascending process of the epipterygoid for a short distance, effectively separating the quadrate from the epipterygoid.

The great extent of the proötic process of the epipterygoid, and the lack of persistent contact between the epipterygoid and pterygoid differentiate this genus sharply from *Eryops*.

The braincase (based primarily on sectioned skull MCZ 1694): In general, the braincase (Fig. 7) of *Tersomius* is similar to that of other labyrinthodonts in having two main areas of endochondral ossification, the anterior sphenethmoid and the posterior otico-occipital. Dorsally and ventrally the endochondral bone is covered by dermal ossifications of the skull roof and palate. The lateral walls in the region of the basicranial articulation are less ossified than in *Eryops*, but otherwise most features are similar to those of that genus.

The exoccipitals form the occipital condyles and the side walls of the posterior portion of the braincase. They are fused ventrally, except for the posterior 2 mm. There is no bony basioccipital, but a groove dorsal to the point of fusion of the exoccipitals was evidently occupied by the cartilaginous precursor of this bone. Whether the basioccipital cartilage continued to the surface of the condyle cannot be determined from the shape of the exoccipitals, but the structure of the atlas suggests that there was no medial area of articulation with the occipital condyle, and hence that this structure was double. The dorsal margin of the foramen magnum is not preserved in the sectioned material, so it is not possible to determine whether the exoccipitals joined one another dorsally, as in *Eryops*, or whether there was a separate supraoccipital. Dorsally this area is covered by the postparietals which extend lappets on either side of the foramen magnum over the posterior surface of the exoccipitals.

The exoccipital extends forward from the condyle approximately 7 mm ventrally, indented above by the basioccipital trough. Dorsolaterally the exoccipital terminates 2½ mm anterior to the tip of the condyle. Just anterior to the condyle are three or four foramina. There are two distinct ventral foramina, one ahead of the other, just above the basioccipital groove. The posterior one opens posterodorsally, and the anterior one posteroventrally. From their position it is evident that they were passages for branches of the XIIth nerve. Dorsal to these openings, there appear openings in each of two successive half-millimeter sections, extending directly laterally. It is not possible to tell whether these represent two separate openings, or the extremities of one large fenestra. It (or they) presumably provided passage for a further branch or branches of the hypoglossal nerve. Anterior and dorsal to these openings is a small foramen, perhaps for a small vein.

The otic region is preserved only on the right side of the specimen sectioned. It does not appear to be divided into separate opisthotic and proötic ossifications. The ventral anterior portion of the otic capsule is either not ossified, or simply missing in this specimen. Since the anterior vertical semicircular canal is partially enclosed in bone, and at least the dorsal margin of the fenestra ovalis is present, the missing portion of the otic ossification cannot be equated with the entire proötic. This region of the braincase is also poorly ossified in other genera of dissorophids (DeMar, unpublished thesis). The otic ossification is more laterally directed than in *Eryops*, and is not in contact with the exoccipital except at its posterodorsal margin. Laterally and ventrally there is a cleft between the exoccipital and otic bones that accommodated the vagus nerve, as well as the IXth and XIth nerves and the jugular vein. Beginning anteriorly about 4½ mm in front of the end of the condyles, this passage extends posteriorly to open behind the otic capsule. This cleft was certainly closed ventrally with cartilage.

The posterior wall of the otic capsule extends dorsally and laterally as the paroccipital process to meet the tabular bone. This process forms the ventral margin of the posttemporal fossa, dorsally and laterally bordered by the tabular, and medially by the postparietal. This opening continues anteriorly for 4 mm before entering the cranio-quadrate passage lateral to the braincase. There is little variation in the dimensions of the posttemporal foramen throughout its length. The fenestra ovalis is located a millimeter or so in front of the rear wall of the otic capsule, beneath the paroccipital process. It is about a millimeter in diameter. Anteriorly it is bordered by bone only dorsally. There is also a foramen in the medial wall of the otic capsule, just anterior to its rear border. Perhaps, as in some lizards (Gaupp, 1900), this opening was occupied by a perilymphatic duct connected with the passage for the vagus nerve. No such opening has been observed in *Eryops*. The dorsal medial wall of the otic capsule turns medially anterior to the fenestra ovalis and forms the lateral wall of the braincase. The passage for the VIIIth nerve was somewhere anterior to this point, but its exact location cannot be determined. Dorsally the otic bones almost meet one another in this area. How much of the dorsal covering of the braincase was formed by the otic bones cannot be determined since the upper surface of the specimen sectioned is missing in this area.

Only the posterior and dorsal portions of the inner surface of the otic capsule are preserved. Dorsal to the fenestra ovalis there is a groove in the roof of the capsule for the posterior vertical semicircular canal. The groove extends anteriorly and medially. In front of the fenestra ovalis this groove continues, turning somewhat laterally, and becomes enclosed ventrally by bone. This is evidently the position of the anterior vertical semicircular canal. Anterior to this point, only that portion of the otic capsule beneath the posttemporal foramen is preserved. There is no direct evidence for the horizontal semicircular canal.

A ventral pocket medial to the fenestra ovalis was evidently occupied by the sacculus and utriculus.

The lateral walls of the braincase are unossified between the otic bone and the sphenethmoid. Nerves IV through VII presumably left the brain through this gap. Anterior to the termination of the exoccipital, the base of the braincase is formed by the parasphenoid, presumably covered by a portion of the cartilaginous basioccipital.

The posterior margin of the basisphenoid is 3 mm anterior to the end of the exoccipital. The basisphenoid has a groove which corresponds with the basioccipital groove in the exoccipital. This may mark the anterior extension of a persistent notochord. The basisphenoid extends as a stout bar across the parasphenoid, exceeding this bone in width anteriorly. The lateral edges are thickened where it is in contact with the pterygoids. The anterior medial portion of the bone is pierced to a depth of over a millimeter by paired recesses for the rectus eye muscles, much as in *Eryops.* Two small foramina lead from the internal carotids into the recesses in the basisphenoid. A third foramen leads into a canal which traverses the basisphenoid between the recesses, continuing anteriorly through a small dorsal projection of the parasphenoid, and posteriorly extending into or above the groove for the notochord. It may have contained a vein which carried the blood from the eye muscles, although no passages were seen between the eye muscle recesses and the vessel in the sections examined. The blood probably flowed into the hypophysial vein, although the exact location of this vessel cannot be determined due to lack of ossification in this area.

Anterior to the basisphenoid, the parasphenoid forms the bony base of the cerebral cavity. Up to this point the parasphenoid has always been separated from the cranial cavity by either bone or cartilage and so was not described in detail. Before discussing this area, we should return to the construction of the parasphenoid at the back of the skull. This bone is first encountered beneath the exoccipitals, level with the posterior wall of the otic capsules. It widens rapidly to surround the ventral margins of the otic bones and extends dorsally around their lateral walls. The dorsal margin curves ventrally beneath the fenestra ovalis. Whether there was attachment to the stapes cannot be determined since that bone is not present in any of the specimens examined. *Dissorophus multicinctus,* from the Clear Fork, has the parasphenoid partially fused to the base of the stapes. This situation also prevails in *Eryops* and *Edops*. Anterior to the fenestra ovalis, the parasphenoid is in contact with the portion of the otic capsule lying beneath the post-temporal foramen. It is difficult to differentiate the two bones in this area. It is probable that some portions of the bone labeled parasphenoid in Figure 5 B are actually part of the otic capsule.

The dorsal extension of the parasphenoid ends just posterior to the basicranial articulation. Here the parasphenoid extends

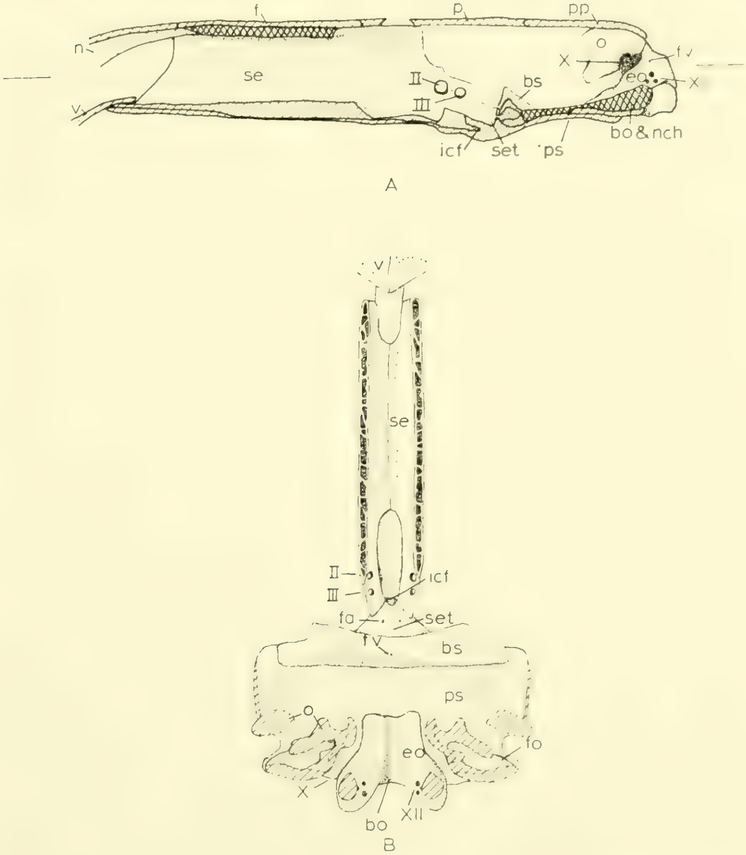

f
p
pp
n
o
X
fv
x
se
II
III
bs
eo
v
bo & nch
icf
set
ps
A
v
se
II
III
icf
fo
set
fv
bs
ps
o
X
eo
fo
X
XII
bo
B

Fig. 7. *Tersomius texensis*. Braincase. A, Median sagittal section (double hatching indicates restored portions); B, Dorsal view of horizontally sectioned braincase, plane of section indicated in A. × 2. Composite drawings.

laterally, in contact with the basipterygoid ramus of the pterygoid, almost to the quadrate ramus. The parasphenoid curves ventrally across the area of the basicranial articulation, tapering in width anteriorly. The internal carotid arteries enter the parasphenoid just posterior to the articulation. At the point where they enter, they are separated by 6 or 7 mm. They proceed medially forward, immediately beneath the basisphenoid. The canals for left and right internal carotids join one millimeter beyond the end of the basisphenoid. At their juncture, a small bone is present in the canal, separating it into dorsal and ventral channels; within a millimeter, however, this bone is gone and the canal opens dorsally.

Throughout the area of the basicranial articulation the parasphenoid is considerably thicker than it is posteriorly. This thickened area continues anteriorly up to the point where the carotid arteries pass out of the bone. The parasphenoid diminishes in width to about 3 mm anterior to the basicranial articulation. Just anterior to the basisphenoid, the parasphenoid has a small dorsal extension pierced by the foramen that runs between the recesses for the eye muscles in the basisphenoid. Anterior to this dorsal extension the parasphenoid is oval in cross section for 2 mm, at which point the internal carotids leave dorsally. The pituitary was apparently housed just anterior to the basisphenoid, although there is no evidence of a recess for this organ in either the basisphenoid or the parasphenoid. Vessels extend dorsally from the internal carotids in this region; presumably these vessels passed dorsally into a cartilaginous sella turcica. Anterior to this point a trough (a millimeter deep and 1½ mm wide) is formed in the parasphenoid. Anteriorly the walls of the trough are reduced and the parasphenoid continues forward, shaped as a bar, dorsally concave. Within 2 or 3 mm of reaching the vomers the dorsal depression vanishes.

In front of the pituitary, the braincase is again walled laterally by bone. Arising from the dorsolateral margins of the parasphenoid and extending anteriorly to the vomers are the paired sphenethmoid bones. In cross section the sphenethmoids form a V-shaped trough. As viewed laterally, each bone is in the shape of a trapezoid, whose top approaches the skull roof. Cartilage probably joined the sphenethmoid to the basisphenoid, with openings for the eye muscles and various cranial nerves.

Just ahead of its posterior extremity, the sphenethmoid is pierced by two pairs of foramina. The anterior openings could have accommodated the optic nerve and probably the ophthalmic artery, since the openings are quite large. The posterior pair presumably allowed passage for the oculomotor nerve.

The sphenethmoids are separated ventrally by the parasphenoid for a distance of 6 mm, beyond which they are in contact until they come within 2 or 3 mm of the vomers, where they are again separated by the parasphenoid. Where the sphenethmoids approach the skull roof, they are separated from it by a narrow space, evidently filled with cartilage in life. It appears that this cartilage continued medially joining the sphenethmoids dorsal to the cranial cavity. This cartilaginous strip made contact with the postfrontals and frontals. The frontal bone bears a ridge just lateral to the braincase, which it probably served to strengthen. This ridge continues on beyond the end of the sphenethmoid almost to the ridges surrounding the nasal capsule.

In cross section it can be seen that the sphenethmoids are composed of external and internal sheets of very thin bone, joined by numerous struts. The inner layer of bone gives a more rounded cross section than the external layer, especially toward the anterior end of the braincase. There is no trace of any medial division such as is present in *Trematops*.

The sphenethmoid is very different from that of *Eryops*. In *Tersomius* the bone is obviously paired, thin and fragile, and with no median partitions or grooves to separate the olfactory nerves and associated vessels. In *Tersomius* the parasphenoid helps to support the sphenethmoid, while in *Eryops* it is a mere accessory to the sphenethmoid, which is the most massive element in the skull.

The most obvious distinction between the braincases of *Eryops* and *Tersomius* is the anterior position of the pineal opening, in the latter, relative to the opening for the optic nerve and the position of the pituitary. The floor of the braincase is much thinner in *Tersomius* than it is in *Eryops* or *Edops*.

Running near the dorsal extension of the parasphenoid for some distance, in MCZ 1694, are two ossified tubes. These passages appear first just in front of the anterior termination of the right exoccipital, above the disarticulated proötic process. They continue anteriorly, moving medially to lie between these processes. They can be traced anteriorly as far as the confluence of the carotids and are most clearly visible in the area of the basisphenoid. The more lateral of the two is about half a millimeter in diameter and almost solid, with a hole less than an eighth of a millimeter in diameter through the middle. The medial vessel is somewhat larger and has very thin walls. The pair are probably the vena capita lateralis (medially) and the supraorbital branch of the stapedial artery (laterally).

Mandible: Each lower jaw is composed of nine dermal bones and the articular. On the lateral surface are exposed the angular, surangular, dentary, coronoid, splenial, postsplenial and articular. The largest bone is the dentary, extending from the symphysis to the coronoid process. A narrow strip of splenial and an even smaller area of the postsplenial separate it from

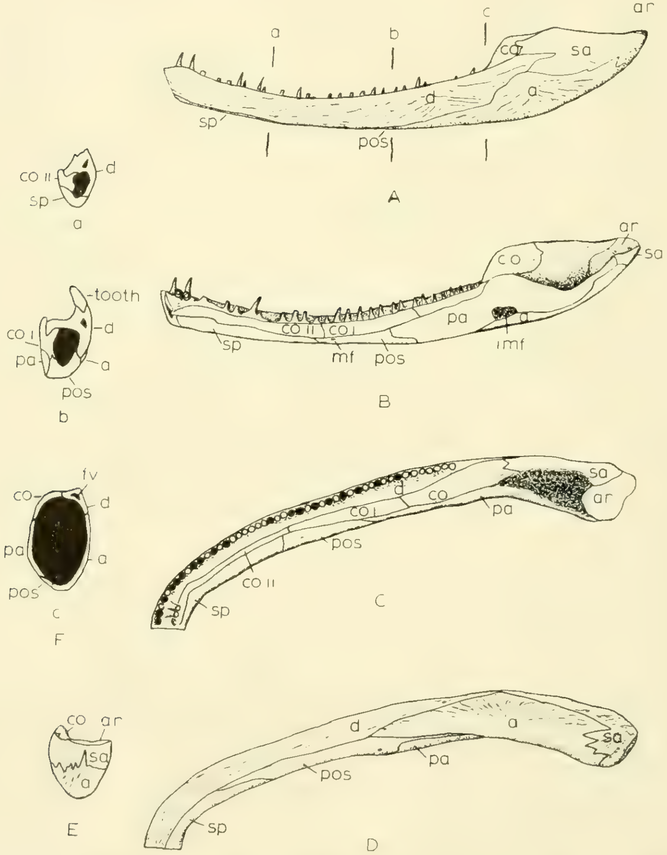

a
b
c
ar
co
sa
d
a
sp
pos
A
co II
d
sp
a
ar
co
sa
tooth
d
co I
pa
a
pos
b
sp
co II
co I
mf
pos
pa
a
imf
B
fv
co
d
pa
a
pos
c
F
sa
ar
d
co
co I
pa
pos
co II
sp
C
co
ar
sa
a
E
d
a
sa
pa
pos
sp
D

FIG. 8. *Tersomius texensis.* Lower jaw. A, Lateral view; B, Medial view; C, Dorsal view; D, Ventral view; E, Posterior view. × 1. F, Transverse sections of jaw at positions indicated in A. × 2. Composite drawings.

the ventral margin of the jaw. Posterior and ventral to the dentary the margin of the jaw is formed by the angular. Dorsal to the angular is the surangular, forming most of the dorsal margin of the coronoid process. The surangular is not sculptured where it is covered by the skull roof. A tiny portion of the articular is visible above the posterior extremity of the surangular. The coronoid lies anterior to the surangular and dorsal to the posterior portion of the dentary, behind the teeth. It forms the anterior portion of the coronoid process.

Medially, the inner surface of the bones discussed on the outside of the jaw can be seen, as well as the precoronoid, intercoronoid, and the prearticular. The dentary is deeply grooved on the dorsal margin, and it is from the lateral edge of this groove that the teeth grow. The lateral ridge covers the base of the teeth to a much greater extent than it does in *Eryops*. The teeth are roughly uniform in size except for those at the very back of the jaw, which are somewhat smaller. The majority of the teeth reach a length of 2 mm, as do those in the upper jaw. There is room for 47 teeth. The pattern of replacement is not clear. The anterior portion of the medial surface of the dentary forms the dorsal one-half or two-thirds of the symphysis and is thickened to support 2 additional teeth, which extend posteriorly and dorsally. These teeth enter the anterior part of the internarial pit.

The three coronoids form a median rim to the groove in the dentary. The precoronoid is very narrow at the symphysis and is recessed beneath the dentary and the splenial. It continues posteriorly for about one-third the length of the jaw and then gives way to the intercoronoid. Behind this is the coronoid which not only forms the anterior portion of the coronoid process but also borders the back of the tooth row. This bone is deflected outward in the anterior portion of the coronoid process. Ventral to the coronoids are the splenial, anteriorly, the postsplenial, pierced by the mandibular foramen, and the prearticular. The splenials have a considerably larger exposure on the medial surface than they do on the lateral. The prearticular is the largest bone exposed medially. Together with a portion of the angular it forms the medial wall of the meckelian fossa. Between these bones, below and anterior to the meckelian fossa, is the inframeckelian fossa. There is some difference in the proportions of these bones and their counterparts in *Eryops*. The splenial is longer in *Tersomius*, while the postsplenial is considerably shorter. The prearticular is also shorter, failing to reach the precoronoid. An even smaller portion of the splenial and postsplenial is visible on the external surface than in *Eryops*.

The articular can be adequately viewed only from above. It is supported by the surangular, angular and prearticular. The articular surface is quite flat but irregular. As in the quadrate, the articulating surface is larger medially than laterally. The bone is quite thick anteriorly where it borders the meckelian fossa.

The meckelian canal continues the entire length of the jaw, and can be seen at the symphysis; it ends before reaching the symphysis in *Eryops*. Dorsal to the meckelian canal is a small canal in the dentary running most of the length of the jaw. Such a canal was not noted in *Eryops*. Failure to find the dental and mental foramina in *Tersomius* is attributed to the small size of the specimens.

Postcranial Skeleton

The only postcranial material associated with *Tersomius* consists of fragmentary atlases, Nos. MCZ 1415, 1694 and 1912. A tibia and humerus collected with AMNH 4719 cannot belong with the skull because of their size. No armor has been found with seven complete or nearly complete skulls and numerous skull fragments. The remainder of the known Permian dissorophids have armor associated with the cranial material. This seems to suggest that the lack of armor is real and not an artifact. (In the genus *Dissorophus*, the presence of a large dorsal shield appears to be the factor responsible for the preservation of well articulated skeletal parts since most of the limbs are laid out directly under the shield.)

OTHER EARLY PERMIAN DISSOROPHIDS

Several additional genera of dissorophids have been described from the Lower Permian of Texas and New Mexico: *Broiliellus*, *Dissorophus*, *Alegeinosaurus*, *Cacops* and *Aspidosaurus*. DeMar has recently reviewed these genera, known primarily from the Clear Fork group, and classified them on the basis of their armor. His description of the armor is summarized here to facilitate comparison with the armor of the species from the Wichita group, which are described below.

Broiliellus has a single plate of wide armor per segment; the center of each plate is located between adjacent neural arches.

Frequently, a ventral flange projects from the center of the armor plates and either extends between adjacent neural arches, or enters slits in the ends of the neural spines. There are 13 or 14 such plates of uniform size, which are ornamented like the bones of the skull roof. Each plate is in contact with the one fore and aft, but adjacent plates are neither fused nor imbricated. *Broiliellus texensis* is known primarily from the Clyde Formation; a second species, from the Arroyo Formation, is being described by DeMar.

Dissorophus has two layers of wide armor plating; the internal layer is similar to that of *Broiliellus* except that it extends for seven or eight more segments. Dorsal to and alternating with this armor is a second set of plates of approximately the same size and shape. The internal shields are not ornamented where they are covered by the external series. Several anterior segments are covered by a continuous sheet of armor, composed of shields from both series in an irregular manner. None of the shields is fused to the neural spines.

Alegeinosaurus and *Cacops* differ from *Broiliellus* and *Dissorophus* in having a narrow internal series of armor which appears to be an outgrowth of the neural spines, and a narrow external series. The two series are related to each other in the same manner as are the external and internal series in *Dissorophus*. There are 15 vertebrae so armored in *Cacops*; the number is not known in *Alegeinosaurus*.

More variation is encountered in *Aspidosaurus* than in the other genera. The type species, *A. chiton*, has neural spines expanded into narrow sculptured shields, some, but not all, of which overlap the shields of the preceding vertebrae. There is only one layer of armor, and the number of vertebrae which are covered is not known. *A. glascocki* has massive armor of a similar nature to that of *A. chiton*, but apparently not imbricated. *A. apicalis* and *A. crucifer* are known only from isolated armored neural spines. The latter species gives the impression of possessing an external layer of armor (although none has been found) since the anterior and posterior margins of the plates are not sculptured. A number of very large armored neural spines, several of which are in the collection of the Museum of Comparative Zoology (Plate 1), have been associated with this genus, but these spines are much larger than are the entire vertebrae of any other dissorophids.

DeMar classified these genera in two subfamilies based on differences in the armor. *Dissorophus* and *Broiliellus*, with broad

TABLE 2

Cranial Dimensions of Permian Dissorophids

	Broiliellus brevis MCZ 1424	*Dissorophus angustus* MCZ 1695	*Brevidorsum profundum* MCZ 3250	*Aspidosaurus novomexicanus* YPM 810	*Conjunctio* sp. MCZ 2369
Length of cranium to extremity of quadrate	68	—	—	—	—
Length of cranium to foramen magnum	58	—	—	—	—
Greatest depth of skull in front of otic notch	16	23	24	29	18
Greatest width of cranium between quadratojugals	57	65	56	64	66
Least width of skull table dorsal to otic notch	39	39	45	53	39
Least width between orbits	16	—	21	26	21
Transverse diameter of orbits	13	—	13	—	17
Longitudinal diameter of orbits	18	—	21	—	23
Distance from center of orbit to quadrate	39	—	39	—	—
Distance from center of orbit to front of skull	29	—	—	—	48
Distance of pineal from foramen magnum	15	—	18	24	18
Back of orbit to front of otic notch	9	8	9	11	6

Dimensions of specimens are to the nearest millimeter.
Measurements taken from projections onto a flat surface.

armor plates not fused to the neural spines, were placed in the subfamily Dissorophinae. *Cacops*, *Alegeinosaurus* and *Aspidosaurus*, with narrow armor fused to the neural spines, were placed in the Aspidosaurinae. DeMar felt that the nature of the armor probably indicated that it had developed separately in the two groups. Separation of the two subfamilies is also suggested by the nature of the sacral ribs; there is a single pair in *Dissorophus*, but *Cacops* has two pairs. The remainder of the postcranial skeleton is not sufficiently known for comparison throughout the family. All of the armored genera have a pattern of ridges surrounding the orbits and bordering the skull table. This pattern differs somewhat in the two groups, but the differences are not as diagnostic as those observed in the armor. Both *Cacops* and *Dissorophus* have the otic notch closed posteriorly, while it is open in the remaining genera.

DeMar described two new genera, but neither is well enough known to place in either subfamily. The same is true of the Russian genus *Zygosaurus*.

BROILIELLUS Williston 1914

BROILIELLUS BREVIS[1] sp. n.

Figures 9, 10 and 11

Type: MCZ 1424, complete skull with lower jaws; partial postcranial skeleton including 12 vertebrae, 9 armor plates, 9 ribs, left and right cleithra and scapulae, fragments of the clavicles and the left humerus.

Referred specimen: MCZ 3272, partial skull and fragments of both lower jaws. An almost complete pelvic girdle, a pair of sacral ribs and the proximal portion of the left femur are possibly associated.

Locality: Both specimens were collected from the Archer City bone bed, one mile southwest of Archer City, Archer Co., Texas.

Horizon: Putnam Formation, Wichita group, Lower Permian.

Collectors: MCZ 1424, collected by Witter, 1936; MCZ 3272, collected by Romer, 1961.

Diagnosis: Dissorophid possessing a single layer of narrow armor plates, not fused to vertebrae. Skull similar to that of *Broiliellus texensis*, except for shorter skull table posterior to orbits. Open otic notch.

---

[1] *Brevis:* from the Latin meaning short in space or time, in reference to the shortness of the armor plates.

Description: The skull of *Broiliellus brevis* (Fig. 9) differs from that of *B. texensis* in having a shorter skull table behind the orbits, and shallower otic notches. These features are shared with *Tersomius* and the Pennsylvanian dissorophids. The tabulars descend slightly toward the quadrates, but do not close the notches behind. The ornamentations on the skull roof are

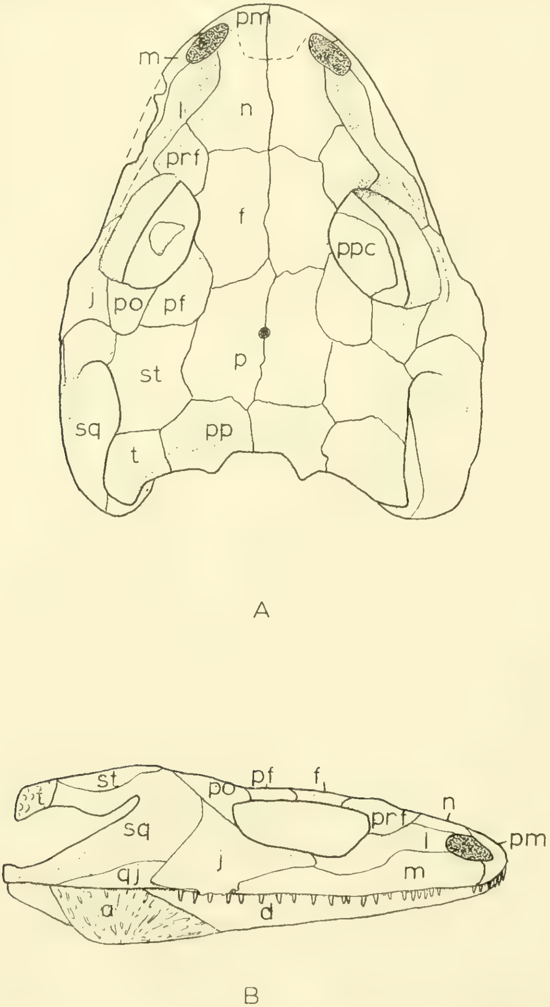

pm
m
l
n
prf
f
ppc
j
po
pf
p
st
sq
pp
t
A
st
t
po
pf
f
n
prf
pm
l
sq
j
m
qj
a
d
B

FIG. 9. *Broiliellus brevis.* MCZ 1424. A, Dorsal view of skull; B, Lateral view of skull. × 1.

in the same positions as those in *B. texensis*, but are slightly less pronounced. The jugal, as noted in *B. texensis* by Williston, has a projection from its ventral surface, in this case extending across the maxilla and quadratojugal to the level of the tooth row. There are prominent ossifications in the orbits, essentially the same as in *B. texensis*, and presumably having the same configuration in life as the ossifications in *Tersomius*.

Between the type and the referred specimen, almost the entire palate can be determined (Fig. 10 A). As in *B. texensis*, there are flanges on the posterior extremity of the parasphenoid for muscle attachments. All the paired bones of the palate are covered by a thick shagreen of tiny teeth. The anterior portion of the vomers ascends to the skull roof, as in *Tersomius*. A single fang was seen projecting from each vomer and palatine bone, but the ectopterygoid tooth and, in fact, the major portion of the ectopterygoid bone are covered by the lower jaws in the type, while this region is missing in the referred specimen. The internal nares are somewhat longer and considerably narrower than they are in *Tersomius* or *Cacops*. The internal nares of a specimen of *Broiliellus texensis* from the Belle Plains, MCZ 1747, are also long and narrow. In the referred specimen of *B. brevis*, the dorsal surface of the palate is visible and discloses a dorsally projecting rim on the vomer and palatine along the medial margin of the internal nares, similar to that observed in *Tersomius*. The ventral projection of the jugal is visible in palatal view. There is room for 39 teeth in the maxilla and 13 in the premaxilla; each tooth is a simple pointed peg, reaching a length of one or two mm. The right stapes is present, extending from the anterior corner of the otic notch to the lateral margin of the parasphenoid plate. None of the braincase is visible.

The jaws are clearly exposed in ventral and lateral views. They are distinctive in two respects. The lateral surface of the angular is very deeply sculptured, particularly in the type, in contrast to the dentary. Ventrally the angular has a projection considerably beyond the remaining surface of the bone. The jaws of other species of *Broiliellus* have not been described in any detail, so comparison is not possible.

The block containing the skeletal material (Fig. 10 B) was in contact with the skull of the type and the fragments were more or less in their natural position. The armor plates are somewhat disturbed and lie to one side of the vertebral column. The armor differs from that of *Broiliellus texensis* in being very narrow; the widest segment is only about 12 mm across, compared with a cranial width of 54 mm. In *B. texensis*, the armor is over half the width of the skull. The structure of the armor, however, is essentially similar to that species — a single, unfused, transversely elongated segment for each vertebra. The plates average about 3 mm in length, although there is some irregularity. They narrow from 12 to 8 mm in width in the first six preserved shields. The most anterior shield is rounded in front, but this may be an artifact of preservation and does not necessarily indicate an anteriormost position in life. The plates do not appear to overlap, but are in close contact. Only one shield, the 8th in the series, is visible from below; it does not appear to bear a ventral flange. If the shields are in place along the length of the column, there is room for 4 more plates in front, making a total of 13. Whether there were more posteriorly cannot be determined. There are 13 or 14 armor plates in *B. texensis*.

Approximately 12 vertebrae are preserved in the block. The anterior 3 show only the neural arch, truncated, and the right transverse process. In related genera, the transverse processes of the first 2 vertebrae are modified; apparently these vertebrae are missing in this specimen, since the first vertebra in the block has transverse processes similar to those of the more posterior vertebrae. The last 3 vertebrae show neural arches, intercentra and possibly pleurocentra, although the units are slightly disarticulated. The vertebrae in the middle of the block are covered by other bones. In the exposed vertebrae the neural arches are quite broad and the transverse processes are prominent. They differ little from the vertebrae in other dissorophids in which armor is present, but not fused.

Seven ribs are visible on the right side, all in ventral view. These are attached to the 2nd through 8th vertebrae in the block, and so presumably are the 4th or 5th through 10th or 11th ribs in the animal. Only the proximal 15 mm of each is preserved. The ribs are uniform slats, of approximately equal width throughout their length. The posterior edge of each is overlapped by the rib to the rear. The proximal ends of the ribs are little if any differentiated from the shaft, and have a flat articulating surface. Two additional ribs are present beneath the vertebral column. It is not possible to determine from which side of the animal they came, nor from what area.

What is visible of the shoulder girdle resembles that of *Dissorophus*, and even more that of *Cacops*. The cleithrum has an expanded dorsal portion extending anteriorly beyond the shaft. The shaft is approximately the same length as the dorsal portion. The clavicles are represented only by a dorsal fragment of each

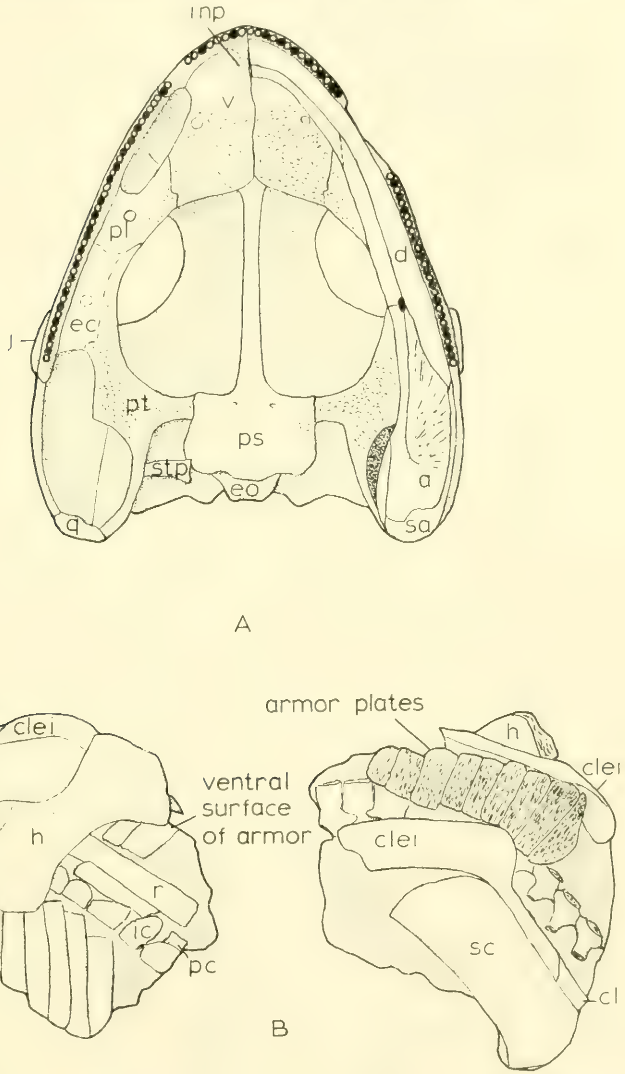

inp
v
pl
ec
j
d
pt
ps
stp
eo
a
sa
q
A
armor plates
clei
sc
h
ventral surface of armor
cl
r
ic
pc
h
clei
clei
sc
cl
B

FIG. 10. *Broiliellus brevis.* MCZ 1424. A, Palatal view with left jaw in place; B, Postcranial material, dorsal and ventral view of block. × 1.

stem. Only the dorsal portions of the two scapulae are preserved. As in *Cacops*, the dorsal anterior margin is slightly truncated for reception of the cleithrum. The left humerus is complete except for the ectepicondylar process distal to the middle of the articulating surface for the radius. The articulating surface for the radius appears less prominent than that in *Dissorophus*. The posterior portion of the proximal articulating surface is expanded ventrally as in other dissorophids, and is recessed at its extremity. The ends are set at an angle of approximately 70°.

A pelvis (Fig. 11) has been associated with the referred skull since they were picked up together, and because it is definitely dissorophid in nature. The pelvis is clearly distinct from that

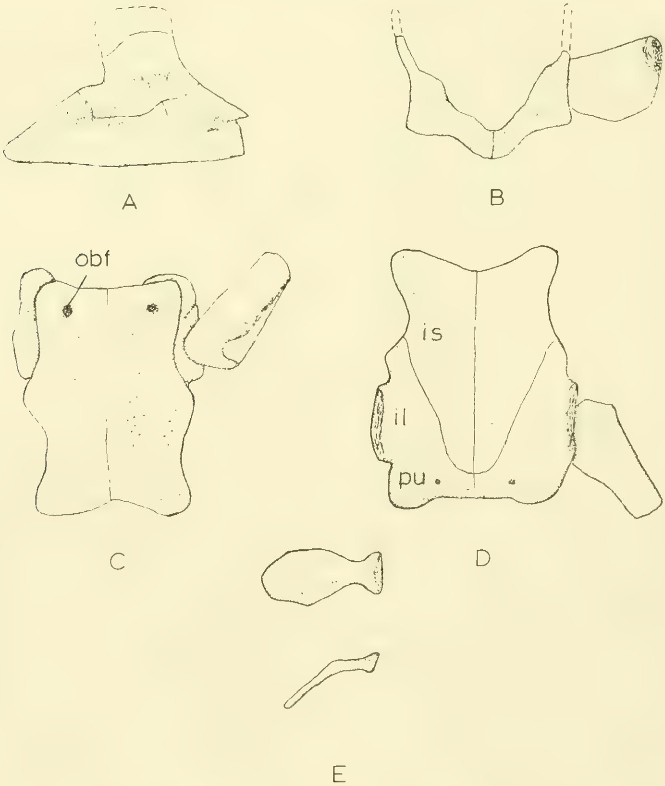


FIG. 11. *Broiliellus brevis*. MCZ 3272. Pelvis. A, Lateral view; B, Anterior view; C, Ventral view; D, Dorsal view; E, Sacral rib. × 1.

of *Dissorophus angustus* (*vide infra*) known from this locality, but the possibility that it belongs to *Tersomius* cannot be completely ruled out since that genus, in which the pelvis is unknown, is common in the Archer City bone bed.

There are very few features in Williston's description of the pelvis of *Cacops* that do not hold for this specimen as well. The proportions of the two differ slightly, with a larger pubis in *Cacops*. There are also minor differences in configuration. In lateral view, the dorsal margin of the ischium is straight in this girdle, while in *Cacops* it is slightly concave and there is a more obvious indenture in the middle of the anterior margin of the puboischiadic plate. Probably due to the relatively small size of the pubes, the obturator foramina are placed nearer the anterior margin than in *Cacops*.

The blades of both ilia are broken off just dorsal to the acetabula. The inside surface of the ilium, as far dorsally as each is preserved, bears no markings for ligamentous attachment of the sacral rib such as are present in *Eryops*. The sutures between the bones are difficult to determine. The sutures separating the ilium from the pubis and ischium can be seen laterally, but only the suture between the ilium and the ischium is determinable medially. The ventral surface of the puboischiadic plate shows no division into its components.

A single pair of sacral ribs was present within the girdle, but neither rib was in place. From their orientation it is not possible to tell which was right and which was left. The sacral ribs are distinct from those of *Cacops*, but resemble somewhat those of *Eryops*. They do not at all resemble those of *Dissorophus multicinctus* described by DeMar. The proximal end of each rib is expanded and appears to have only one surface of articulation with the sacral vertebra. Presumably, as in other dissorophids described, it articulated with both the transverse process of the neural arch and the intercentrum. A short constricted area separates the proximal and distal articulating surfaces. The shaft is curved so that there is about a 45° angle between the surface of the rib articulating with the ilium and the proximal end of the shaft. The distal portion of the rib is expanded dorsoventrally about three times the thickness of the shaft. This portion is large enough to cover the entire breadth of the ilium if the size of that bone is comparable to that of other dissorophids, so it is unlikely that there were two sacral ribs. Only the medial surface of the distal portion is visible due to the fragility of the bones, which made it difficult to clean both surfaces. The central portion is thickened as a continuation of the shaft. There is an additional thickening on the dorsal (or ventral, depending on which is the right rib) margin. Both the dorsal and ventral margins appear to be finished bone.

A fragment of the left femur is attached to the pelvis. The adductor crest is prominent as in all dissorophids. Not enough has been preserved for further comparison.

Discussion: From the structure of the armor and the configuration of the skull of *Broiliellus brevis,* there can be little doubt that this form is ancestral to *Broiliellus texensis,* although differing sufficiently to be considered a separate species.

Two fragmentary skulls described by DeMar, University of Texas nos. 3189-8, both from Thaxton ranch, Clay County, Texas, may belong to this species. According to Romer, this locality is probably in the Admiral Formation, slightly above the Archer City bone bed. The lack of any postcranial material unfortunately prevents definite assignment of these skulls, since it is primarily on the basis of armor that *B. texensis*, *B. brevis*, and *Dissorophus angustus* are differentiated.

DISSOROPHUS Cope 1895

DISSOROPHUS ANGUSTUS[1] sp. n.

Figures 12, 13 and 14

Type: MCZ 1695, partial skeleton, including right rear portion of skull, vertebral column from atlas to third postsacral with ribs and dermal armor, pelvic and pectoral girdles, and limb fragments. This is the only specimen known.

Locality: Archer City bone bed, one mile southwest of Archer City, Archer County, Texas.

Horizon: Putnam Formation, Wichita group, Lower Permian.

Collector: L. I. Price, 1937.

Diagnosis: Dissorophid possessing a complete set of internal dermal plates above the vertebrae, and an incomplete external set, neither fused to the neural spines, neither exceeding in width the distal extremities of the transverse processes of the fourth vertebra. Otic notch not closed behind.

Description: The skull of this animal (Fig. 13) is unfortunately quite incomplete. Only the portion to the right of the midline, behind the orbit, is preserved. What is present resembles the skull of *Broiliellus brevis* in the pattern of ornamentation and the open otic notch. It differs from that species in the much greater depth of the rear portion of the skull relative to the width of the skull table. The distance between the front of the otic notch and the back of the orbit appears to be shorter, relative to other cranial dimensions, in this specimen. It is not possible to determine whether the jugal extends to the margin of the palate since the vertebral column is firmly affixed to the side of the skull. The right rear portion of the palate is also preserved. It is very similar to that of *Broiliellus*, except that the margin is much lower than the basicranial articulation. The pterygoid and ectopterygoid are covered with a

---

[1] *Angustus:* from the Latin meaning narrow, in reference to the narrow armor plates.

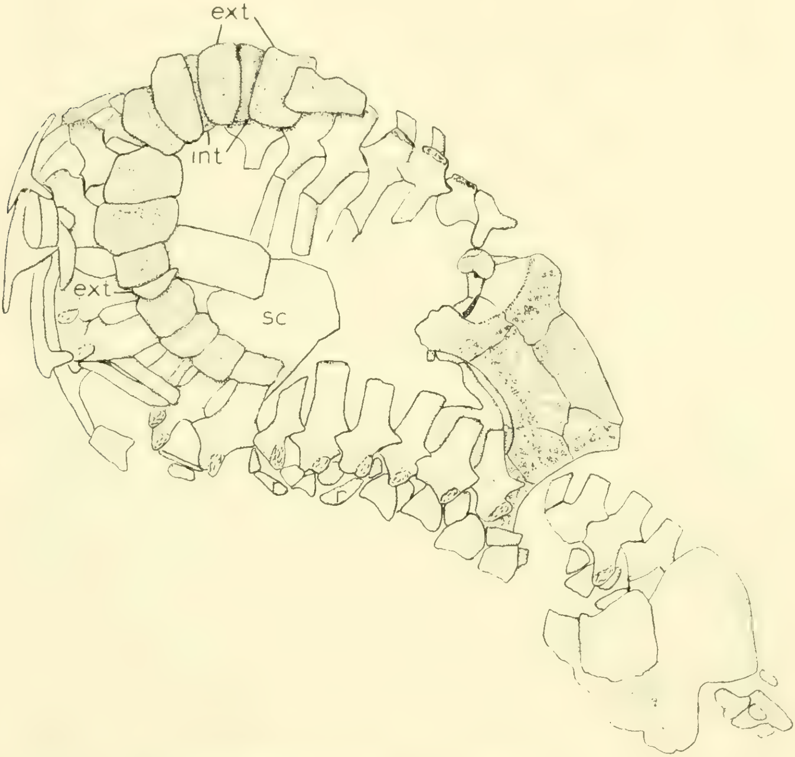


FIG. 12. *Dissorophus angustus*. MCZ 1695. × 1.

thick shagreen of teeth. The muscle attachments on the parasphenoid do not appear quite as prominent as in *Broiliellus*. The basicranial articulation is firmly sutural. The skull is fractured so that the openings for the internal carotids are not visible. The stapes is present, but displaced to the rear. It is imperforate as in other Permian dissorophids.

The occipital region is better preserved than in other dissorophids studied. The major features resemble those of *Eryops* and *Tersomius*. The occipital condyle is distinctly double. As in *Tersomius*, the otic bone is located mostly lateral to the condyles, rather than lying mostly dorsal to these structures, as in *Eryops*. There appears to be a separate ossification, the supraoccipital, medial to the dorsal portion of the exoccipitals. The contact between this bone and either the exoccipital or the otic cannot be seen in the sagittal view.

The skull is broken almost at the midline, giving a sagittal view of the braincase. Most of its features resemble those noted in *Tersomius*. As in *Tersomius*, a ventral cleft separating the otic and exoccipital bones allows passage for the Xth nerve. Anterior to the otic region there is a large gap in the wall of the braincase, the posterior portion of which results from a failure of the otic capsule to ossify completely. In front of this gap, the epipterygoid is functionally a portion of the lateral wall of the braincase. This bone is divided into two portions. An anterior rod arises just lateral to the basicranial articulation and ascends to the skull roof. It slants medially at about a 45° angle to approach the midline of the skull roof. Arising from the base of this anterior rod, the posterior portion of the epipterygoid slopes posterodorsally and slightly medially to approach the otic bone near the skull roof. Medial to the base of the epipterygoid there is a pronounced depression in the parasphenoid anterior to the basisphenoid to accommodate the pituitary and the rectus eye muscles. There is no trace of the sphenethmoid.

The postcranial skeleton (Figs. 12 and 14) is quite well preserved, but preparation was somewhat complicated by the twisting of the vertebral column into a semicircle.

The armor is the most interesting aspect of this species. It is an ideal intermediate between the structure of *Broiliellus* and that of *Dissorophus multicinctus*. No armor was preserved above the first 4 vertebrae, but since the 2nd, 3rd and 4th neural arches are broken off, it is probable that the anterior end of the armor was lost in preservation, rather than missing in the living animal. Armor covers the 5th through 17th vertebrae. There is definitely no armor associated with the 19th vertebra, but the presence or absence of armor on the 18th is difficult to determine since the dorsal portion of the neural spine is missing and this vertebra is at the edge of one of the three blocks of matrix. The 7 posterior armor plates are similar to those of *Broiliellus brevis*. It is not possible to determine whether ventral flanges were present. Between the 13th and 14th vertebrae there is a narrow shield dorsal to the series just mentioned, similar to those of the external series in *Dissorophus multicinctus*. Since the 15th shield is unsculptured on its anterior edge, it is possible that a further small external plate rested here. The internal shields do not appear to overlap to any extent. In front of shield 10 (numbered in Fig. 14 D) there are two plates per segment: an internal plate, homologous to shields 11 through 17, and an external plate, homologous to the shield between plates 13 and 14. Shield 10 appears to consist of one plate of each series fused together, since it overlaps the 11th, but is itself overlapped anteriorly. The most anterior plate, covering neural spines 5 and 6, is anomalous since it overlaps an external shield. It is both narrower and longer than the other plates. Its left edge, and presumably the right also, is broken off. It appears possible that it extended over the 3rd and 4th vertebrae also, since the anterior shield in *Dissorophus multicinctus* is considerably longer than the remainder. The anterior members of the internal series are visible from the side and show distinct ventral flanges. The 7th and 8th shields each have two ventral flanges visible from the left side, extending anteriorly and posteriorly to the 7th and 8th neural spines.

The vertebral column is well preserved in this specimen. There are 26 presacral vertebrae, 1 sacral, and 3 caudals. The first two vertebrae are distinct from the remainder. In lateral view the atlas greatly resembles that of *Amphibamus lyelli*. It consists of a neural arch fused to a cylinder consisting of the intercentrum and possibly the pleurocentra, as in *Cacops* and *Dissorophus multicinctus* (Williston, 1910). Whether, as in those genera, there are two dorsal prongs arising from the centrum is not possible to tell. One projection is situated to the right of the succeeding neural arch, but there is no complement on the left side. That side is damaged to the extent that the midline cannot be determined, so the left side cannot be restored on the pattern of the right. This single prong is

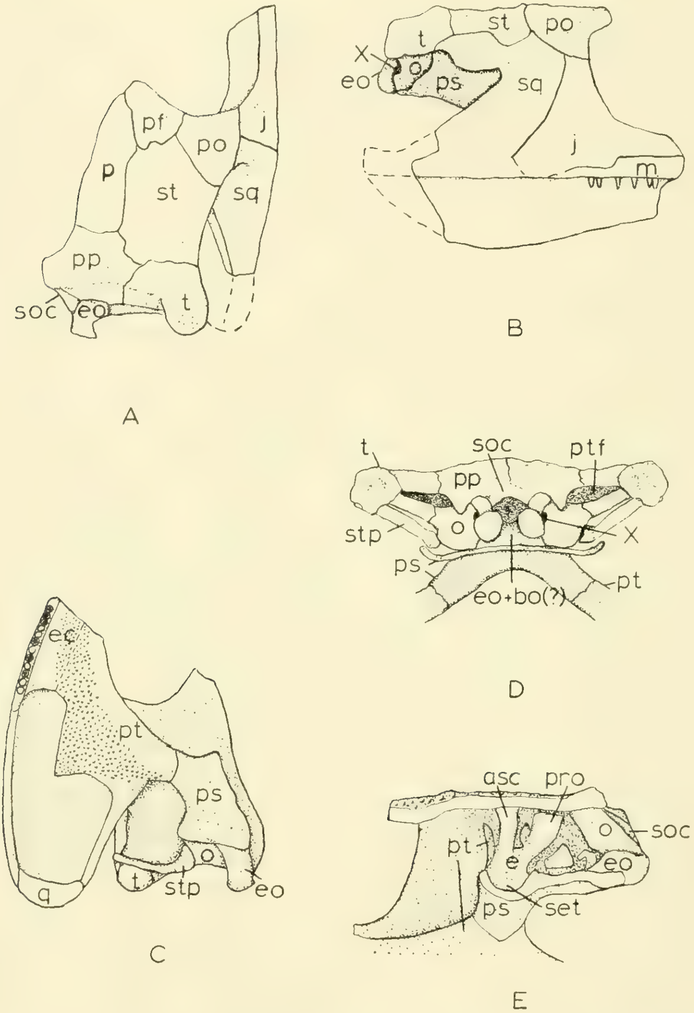

pf
j
po
p
st
sq
pp
soc
eo
t
A
st
po
t
X
o
eo
ps
sq
j
m
B
t
soc
ptf
pp
stp
o
X
ps
pt
eo+bo(?)
D
ec
pt
ps
o
t
stp
eo
q
C
asc
pro
o
soc
pt
e
eo
ps
set
E

Fig. 13. *Dissorophus angustus.* MCZ 1695. Skull. A, Dorsal view; B, Lateral view; C, Palatal view; D, Posterior view; E, Sagittal section of braincase. × 1.

similar to, although smaller than, the neural spines behind it. There are small projections extending anteriorly and posteriorly just above the neural canal that aid in articulating the atlas with the condyles and the axis. The nature of the surface articulating with the occipital condyles is impossible to determine. A lateral projection of the neural arch forms a weak transverse process which apparently did not bear a rib. A small fragment of bone in front of the atlas may have been part of a proatlas.

There are also modifications in the second vertebra; the transverse processes are large and blunt, and presumably did not bear ribs. No free pleurocentra are visible between the 2nd and 3rd vertebrae, but there is a separate intercentrum. The anterior zygapophyses are only poorly developed but the posterior ones are like those of the remainder of the column. The remaining vertebrae are quite uniform as far as can be judged, except for diminishing somewhat in size behind the sacral region. The 3rd through 30th vertebrae bear strong transverse processes, decreasing only slightly in length posteriorly. They extend horizontally and obliquely posteriorly as far as the margin of the dorsal shields. The articulating surface for the ribs is straight and faces slightly ventrally and posteriorly. On the first 21 vertebrae, it is as large as the articulating surface of the ribs. It becomes smaller in the sacral region. The neural arches are consistently 9 mm long from the 5th to the 19th vertebrae; they decrease gradually to a length of 5 mm behind the sacrum. In each of neural spines 15, 16 and 17 there is a vertical groove in the lateral surface for most of its length.

The ventral units are concealed by the ribs or other bones in the anterior region of the column. Where visible, the anterior intercentra do not appear to bear articulating facets for the ribs. In the region of the sacrum the ribs do articulate with the intercentra, but the intercentra are not modified for their attachment. The intercentra are uniformly crescent-shaped throughout the column, as they are in *Cacops*. The pleurocentra are nowhere clearly visible.

The ribs are fairly well preserved. None were found with the first two vertebrae, and from the nature of the transverse processes it seems probable that there were none. This is also the condition noted in *Amphibamus lyelli*; the condition in other dissorophids is not certain. Ribs are present on the 3rd through 19th vertebrae. These ribs appear single-headed, with little or no articulation with the intercentra. A number are in position, resting directly on the transverse processes, and there is no room for separate capitular heads. The length increases rapidly from the 1st to the 5th rib, after which it decreases gradually for the remainder of the column. The first 4 ribs are of uniform width, 4 mm, throughout their length. The 5th through 13th ribs have uncinate processes. The 2nd, 3rd and 4th ribs are covered by the scapula so that the presence of uncinate processes cannot be determined. The processes are all located about the same distance from the articulating surface, and so gradually approach the distal extremity of the rib. The processes increase in length from the 5th rib posteriorly, reaching a maximum length of 7 mm in the rib for the 11th vertebra, and decreasing sharply in the 12th.

No ribs are preserved on the 20th through 25th vertebrae. Presumably the ribs in this area were similar to those just anterior. The proximal portion of the right rib of the 26th vertebra is present and articulates with both the transverse process and the intercentrum. The sacral ribs, on the 27th vertebra, are also articulated with the intercentrum. They are similar to, although larger than, the sacral ribs in *Broiliellus brevis.* There appears to be less than a 45° angle between the proximal end of the shaft and the surface of articulation with the ilium. This surface is expanded ventrally to about twice the width of the proximal end of the shaft. It is not quite as extensive as the sacral rib in *Dissorophus multicinctus*, but the surface of articulation is larger than that in *Broiliellus.*

The ribs on the 28th and 29th vertebrae are similar in size to those on the 26th, and each has a separate area for articulation with the intercentrum, and with the neural arch. These ribs are not at all modified to articulate with the pelvis.

The girdles are fairly well preserved. The right scapulocoracoid is complete although the dorsal portion is covered by the vertebral column. Except for its smaller size, nothing distinguishes the scapulocoracoid from that of *Dissorophus multicinctus.* The dorsal margin of the left scapula is preserved and shows a truncated anterior margin, similar to that noted in *Cacops.* A fragment of the right cleithrum lies beneath the vertebral column. This bone is apparently expanded dorsally in a manner similar to that seen in other dissorophids. The stem is not preserved. Both clavicles are preserved. In configuration and extent they are similar to the clavicles of *Cacops* and *Dissorophus multicinctus.* The dorsal extent of the stem cannot be determined. The interclavicle is present, but its configuration cannot be determined since preparation would necessitate destruction of the clavicles.

The right humerus was found in place in the glenoid cavity. The bone was crushed, however, and presents no details worth describing. Several toe bones were found in the vicinity of the forelimb. The largest and most complete is 6 mm long. They are in no particular order.

The left half of the pelvic girdle is fairly well preserved. It resembles most closely the pelvis of *Dissorophus multicinctus* (MCZ 2122) now being studied by DeMar. It differs significantly from the pelvis associated with *Broiliellus brevis*, and also from that of *Cacops*. The puboischiadic plate is much more upright than in these genera. It is less erect, however, than that of *Eryops*. The ilium is expanded more in an anterior-posterior direction and also more dorsoventrally than in *Cacops*. Its extent is approximately the same as in *Dissorophus multicinctus*.

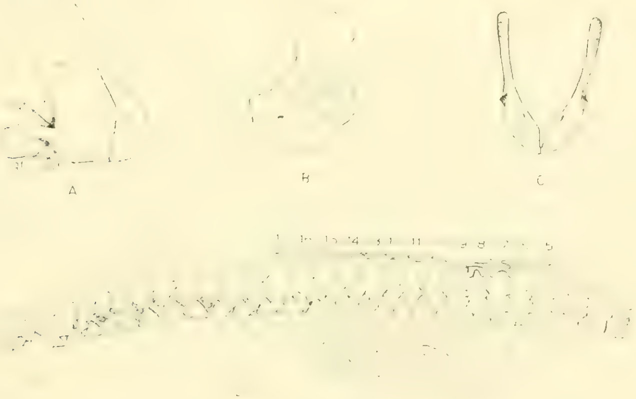


FIG. 14. *Dissorophus angustus*. MCZ 1695. Postcranial skeleton. A, Lateral view of pectoral girdle; B, Lateral view of pelvic girdle; C, Anterior view of pelvic girdle, right side restored from left; D, Vertebral column, ribs and armor. × 1/2.

The posterior portion of the ischium is missing. A crushed fragment of the left femur was present in the acetabulum, but no other material from the hind limb was preserved.

Discussion: The pattern of armor of this specimen is clearly intermediate between that of *Broiliellus* and that of *Dissorophus*, as is the number of segments covered. While the posterior shields are generally like those of *Broiliellus*, the anterior region is *Dissorophus*-like in pattern. The narrowness of the armor reflects the primitive condition observed in *B. brevis*. The possession of two flanges rather than a single ventral flange projecting from the anterior ventral series is unexpected in an ancestor of *Dissorophus multicinctus*, but the high degree of variability in other aspects of dissorophid armor, noted by DeMar, suggests that this is not an important distinction. In other respects this species is an excellent ancestor of *Dissorophus multicinctus.*

An interesting aspect of the armor of this species is its resemblance to that of *Cacops.* If the armor were fused to the neural spines, there would be little to differentiate the two. One point of distinction is the composite anterior shield, resembling that of *Dissorophus multicinctus* rather than that of *Cacops,* in which each vertebra has its own separate pair of shields. Other features of the skeleton, such as the number of presacral vertebrae and sacral ribs, serve to differentiate clearly these two genera.

BREVIDORSUM[1] gen. n.

Type species: Brevidorsum profundum.

Diagnosis: Dissorophid possessing ridges around the orbits, but lacking them on the margins of the skull table. Postfrontals and prefrontals not meeting above orbits. Jugal not overlapping quadratojugal or maxilla. Room for 45-55 teeth in each jaw. Otic notch open. Presence of armor not known.

BREVIDORSUM PROFUNDUM[2] sp. n.

Figures 15 and 16

Type: MCZ 3250, partial skull and postcranial material including fragments of both scapulae and cleithra, portions of both humeri, left femur, left tibia and fibula, one or more vertebrae with attached ribs.

Locality: North of the west fork of the Trinity River, Texan Emigration and Land Co., Section 1834, Archer County, Texas.

Horizon: Near Pueblo-Moran boundary, Wichita group, Lower Permian.

Collector: A. S. Romer, 1948.

Diagnosis: Same as for genus.

Description: Most of the right side of the skull is preserved

---

[1] *Brevidorsum:* from the Latin *brevis,* meaning short, and *dorsum* (neuter) meaning back or ridge, in reference to the limited extent of the ridges on the skull.

[2] *Profundum:* from the Latin meaning deep, in reference to the depth of the back of the skull.

(Fig. 15), lacking only the nasal region; only a few fragments of the left side of the skull table and palate are visible. The general characteristics of the skull are those common to all

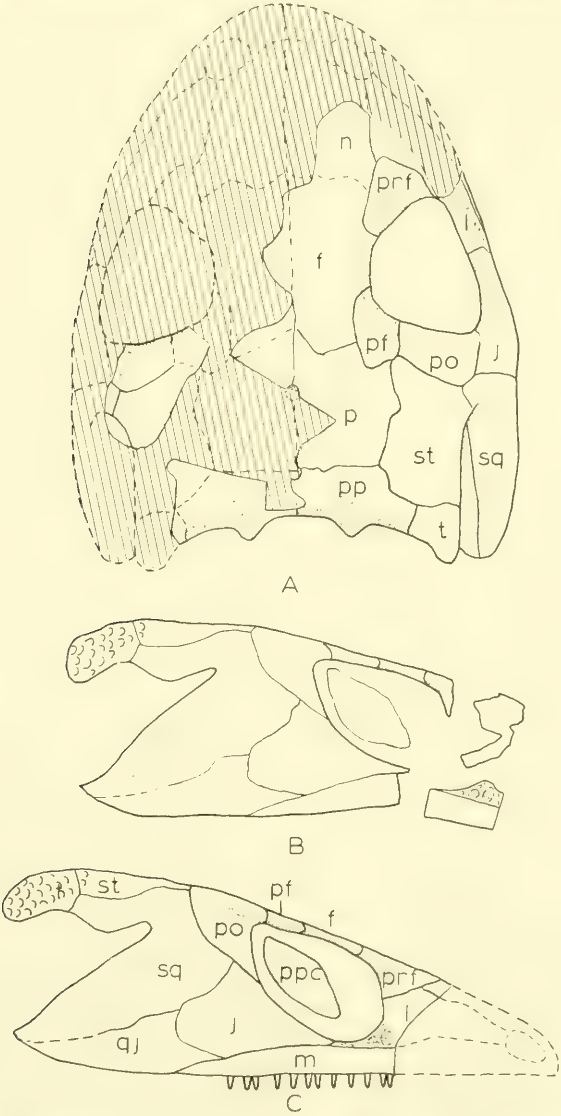

n
prf
l
f
pf
po
j
p
st
sq
pp
t
A
B
st
pf
f
po
ppc
prf
sq
j
l
qj
m
C

FIG. 15. *Brevidorsum profundum*. MCZ 3250. A, Dorsal view; B, Lateral view; C, Lateral view restored. × 1.

Permian dissorophids: a prominent otic notch, open in this genus, and large orbits which gain contact with the frontals. The skull table is somewhat deeper than in the majority of dissorophids, and as a consequence the skull roof descends in a straight line toward the nasal region. The teeth are of the same dimensions as those of most other dissorophids; if the skull were restored using the pattern of other members of the family, there would be room for approximately 51 marginal teeth in each jaw. There is evidence of a bony eye plate in the right orbit. The skull is probably close to adult size, since it is larger than those of other Wichita dissorophids. The closure of the sutures is complete.

The most important characteristic of this skull is the pattern of ornamentation. Ridges surround the orbits and extend onto the nasal region. One ridge lies dorsal to each orbit, arising on the prefrontal anteriorly and passing back across the frontal, postfrontal and onto the postorbital. A second ridge diverges from the first in the prefrontal and extends toward the posteromedial margin of the lacrimal. It terminates at the posterior edge of that bone. A short ridge occurs on the orbital margin of the jugal, but fails to reach the postorbital. In the middle of the postorbital there is a shallow triangular depression, surrounded by slight ridges. This pit is in the same position as a similar feature in *Cacops*. There is also a small pit in the lacrimal just beneath the orbit, and another in the prefrontal. This pattern is essentially the same as that observed in *Dissorophus* and *Broiliellus;* it differs from these genera in lacking ridges on the rear of the skull table. The only ornamentations in that region are small tuberosities on the postparietals and parietals. One character it shares with *Tersomius*, in contrast to *Broiliellus*, is that the jugal does not overlap the maxilla or quadratojugal. The pattern of ornamentation suggests an intermediate condition between the smooth-skulled dissorophids of the Pennsylvanian and *Tersomius*, and the typical genera of the Permian, *Broiliellus* and *Dissorophus*.

The postcranial material is poorly preserved and was freed from the matrix only with great difficulty. The proximal portion of the right humerus is preserved only well enough to identify it as such and note general similarities with other dissorophids. The left femur (Fig. 16 A) is fairly well preserved, lacking only the most proximal portion. The adductor ridge is prominent as is common in dissorophids, but does not extend distally as far as in *Cacops*. The left tibia (Fig. 16 B) is similar to that of

Cacops, but with a narrower shaft. Only the dorsal portion of the left scapula was preserved. It has a slight anterior truncation as was noted in *Broiliellus brevis* and *Dissorophus angustus*. A fragment of the cleithrum is attached. The remaining bones are too fragmentary for meaningful description, or were damaged in removal of the bones mentioned. One or two vertebrae are preserved, but unfortunately lack the neural spines. The dorsal portion of the block was eroded and so determination of the presence or absence of armor is not possible.

Discussion: The characters of this animal as well as its stratigraphic position suggest that it was transitional between the unornamented species of the Pennsylvanian, and *Broiliellus* and

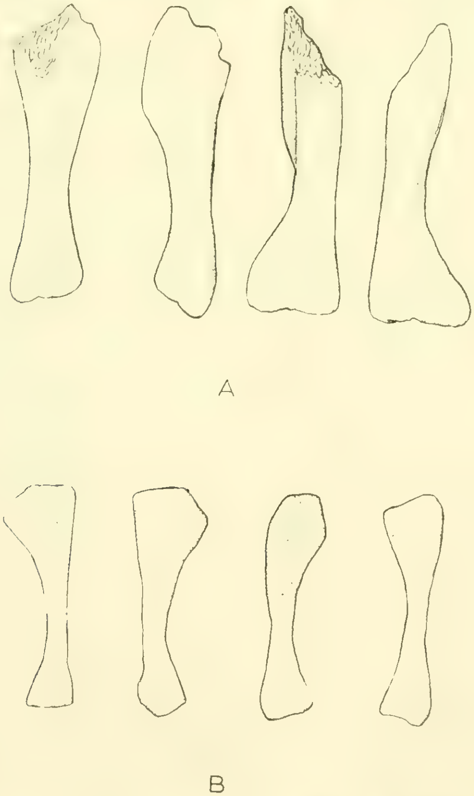


Fig. 16. *Brevidorsum profundum*. MCZ 3250. A, Femur; B, Tibia, in posterior, anterior, lateral and medial views. × 1.

Dissorophus. It seems sufficiently distinct from both of these groups, however, to warrant placing it in a separate genus.

The taxonomic status of several additional species is not clear, and should be discussed before considering the evolutionary pattern of the Permian dissorophids.

ASPIDOSAURUS Broili 1904

ASPIDOSAURUS NOVOMEXICANUS Williston 1911

Figure 17

Aspidosaurus novomexicanus Williston, 1911, p. 20.

Broiliellus novomexicanus (Williston), Langston, 1953, p. 380 (in part).

Type: YPM 810, skull and skeleton. This is the only known specimen.

Locality: El Cobre Canyon, Rio Arriba County, New Mexico.

Horizon: Roughly equivalent to the Moran of Texas, Wichita group, Lower Permian.

Revised diagnosis: Dissorophid with a single layer of narrow armor plates, in the process of fusing to the neural spines. Individual plates not in contact with one another. Some plates longer than others; total number of plates unknown. Open otic notch. Room for 45-55 teeth in each jaw. Twenty-one presacral vertebrae. One sacral rib; anterior ribs with uncinate processes.

Description: Although additional specimens have been referred to this species by Case, Williston and Mehl (1913), and by Langston (1953), they clearly belong to a separate genus and will be discussed under *Conjunctio.* Several changes must be made from the original description of this species, since it was based on an incomplete conception of other dissorophids. A complete description is still difficult due to the fragmentary nature and poor preservation of the specimen.

Both the skull roof and the palate are preserved behind the nasal region, together with fragments of both jaws. All the bones of the skull roof lack their original surface and so no sign of typical dissorophid rugosity can be seen nor denied. A depression in the middle part of the skull table is probably only a result of post-mortem distortion, since the skull as a whole is skewed to the right, and the left side is turned under. The pattern of most of the cranial bones is readily determined and differs little from that of *Dissorophus*, *Broiliellus* or *Tersomius.* It is not possible to determine whether the maxilla and quadratojugal were overlapped by the jugal since the surface of the

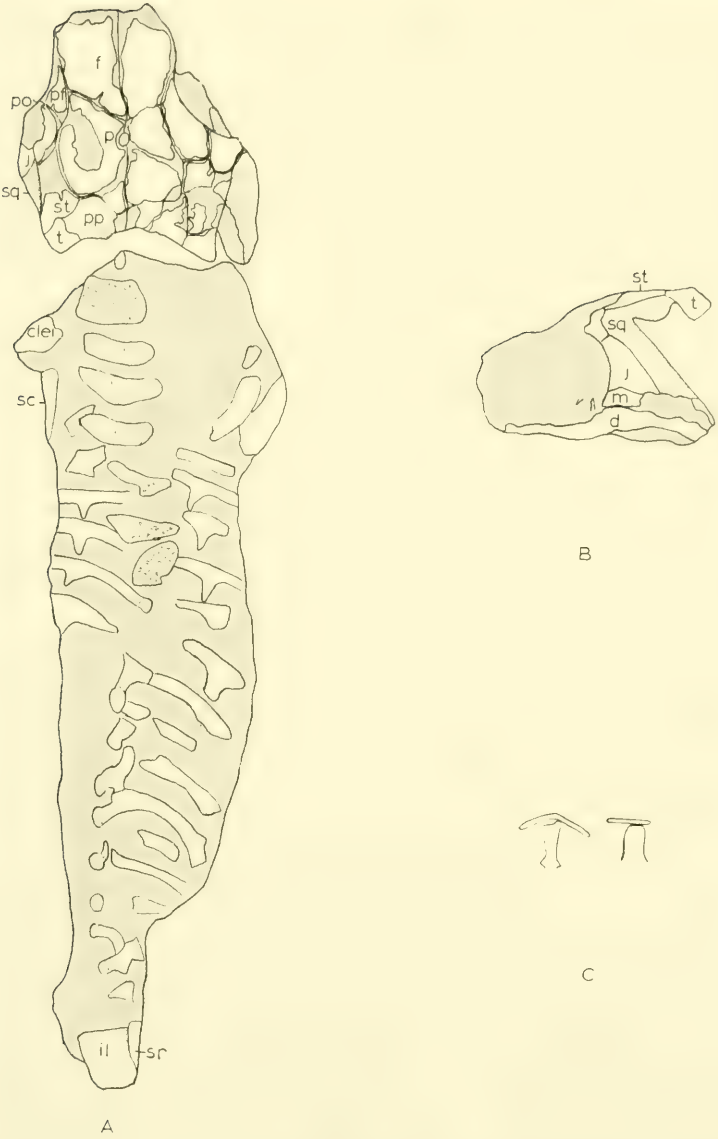

f
po
pf
p
j
sq
st
pp
t
clei
sc
il
sr
A
st
t
sq
j
m
d
B
C

FIG. 17. *Aspidosaurus novomexicanus.* YPM 810. A, Dorsal view of skeleton; B, Lateral view of skull; C, Detail of armor attachment, anterior and lateral views. × 1/2.

latter bone is eroded. The region of the otic notch is well enough preserved to determine with certainty that the notch was not closed posteriorly. The cheek region is relatively deep.

Fragments of both lower jaws are preserved, the left showing one tooth, similar in size to those of *Dissorophus* or *Broiliellus*. There would be room for 45-55 teeth of this size in each jaw. Only the medial portion of the palate is preserved. The basicranial articulation is apparently sutural. The ventral flanges of the parasphenoid, noted in *Broiliellus* for muscle attachment, are not apparent, but this may be due to faulty preservation. A fragment of the left stapes is preserved, but apparently none of the braincase.

A large portion of the postcranial skeleton is present, but it is all poorly preserved. Narrow armor plates are preserved dorsal to the 3rd through 9th vertebrae. It cannot be determined whether there were additional plates. None are fused to the neural spines, but all appear in the process of fusing. The first and seventh plates are longer than the remainder, but none of the plates are in contact with one another. The entire dorsal surface of each plate is sculptured, so there was apparently no external layer of armor. Each plate is in the shape of a very open, inverted V.

There are 21 presacral vertebrae. Their most important feature is the great thickness of the neural spines beneath the armor plates. As was mentioned in the original description, the anterior ribs have marked uncinate processes. The single sacral rib has a wide area for articulation with the ilium. Fragments of the shoulder girdle, one ilium and pieces of the front limbs are present, but the surface is gone from all of the bones.

Discussion: According to Langston and to Romer, the El Cobre Canyon locality where this specimen was found is lower than the typical Abo Formation, i.e., perhaps equivalent to the Moran of Texas. This specimen is hence older than any other armored dissorophid known, with the exception of isolated armor plates from the Moran of Texas. The nearest relationship of this species appears to be with *Aspidosaurus chiton* from the similarity of the armor, since both animals have armor of different dimensions in different regions of the column. Although not attached, the armor of *A. novomexicanus* shows signs of becoming connected, including expansion of the terminal portion of the neural spines. Langston placed this species in the genus *Broiliellus* on the basis of the referred specimens and not the type, which he was unable to study.

ASPIDOSAURUS sp.

Figure 18 and Plate 1

The earliest dissorophid armor known from Texas consists of three neural spines with fused plates from the Moran Formation (MCZ 2740). These were collected by L. I. Price in 1935, one mile northwest of Padgett, northeast part, Wm. Tryndale survey, Young County, Texas. They resemble in a general way the armor associated with the type skull of *Aspidosaurus chiton* from the Arroyo (Broili, 1904). One piece has a longitudinally and transversely expanded dorsal portion in the shape of an inverted V, with pitting over all but the midline of the dorsal surface. Another has only a small expansion of the end of the neural spine; this is sculptured in the mid-portion, but not on the anterior or posterior margins. The spines resemble, respectively, figures 13 and 14 in plate VI of Broili. A third, small shield is expanded transversely, but not longitudinally, and is either not sculptured, or else the surface has weathered off.

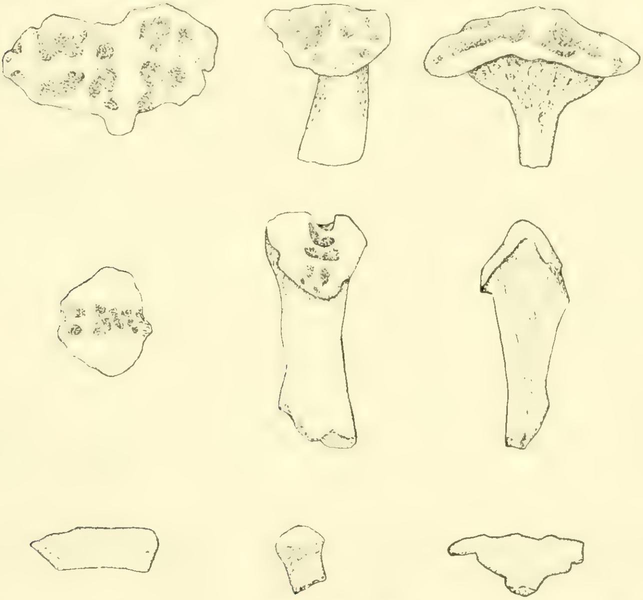


FIG. 18. *Aspidosaurus* sp. MCZ 2740. Three neural spines with fused armor in dorsal, lateral and anterior (or posterior) views. × 1.

Armor of a similar nature has been found in the following additional localities and horizons of the Texas Permian. Putnam Formation: MCZ 1701, Archer City bone bed, Archer County. Admiral Formation: MCZ 2745 and 3162, Briar Creek bone bed, Section 32, Dallas County school land, Archer County. Belle Plains Formation: MCZ 2528, Wm. Mann survey, Section 40, A-271, southwest of Dundee, Archer County; and MCZ 2529, four miles east of Rendham, southwest part of Fayette County school land, Baylor County. In all but the last of these localities, several different shapes of armor are present, but all seem to be within the range of variation of the armor in *Aspidosaurus chiton.*

Other armor, of a much more bizarre nature, is found in considerable quantity at Rattlesnake Canyon in the Admiral Formation (MCZ 1477, Plate 1), and also at Tit Mountain in the Belle Plains (MCZ 2746). The pattern of this armor varies from that observed in *Aspidosaurus chiton* to that of *Platyhystrix.* This type of armor could have evolved from that found in the Moran Formation, but since nothing except the armor is preserved, it cannot even be definitely stated that this animal, or animals, was a dissorophid.

CONJUNCTIO[1] gen. n.

Type species: Conjunctio multidens.

Diagnosis: Dissorophid with a single layer of narrow armor plates, the anterior plates fused to the neural spines; otic notch not closed posteriorly; 70 or more teeth in each jaw. Pattern of cranial ornamentation similar to that of *Broiliellus* and *Dissorophus*, but less pronounced. Jugal overlapping quadratojugal and maxilla. Median rostral fontanel.

CONJUNCTIO MULTIDENS[2] sp. n.

Aspidosaurus novomexicanus, Case, Williston and Mehl, 1913, p. 7.
Broiliellus novomexicanus, Langston, 1953, p. 380 (in part).

Type: CNHM 673, skull and associated postcranial material including femora, humeri, scapulae, pelvis, section of vertebral column and armor. Illustrated by Case, Williston and Mehl, 1913, figure 7.

---

[1] *Conjunctio:* from the Latin *coniunctio* (feminine), meaning a joining together, in reference to the fusion of armor to the neural spines.

[2] *Multidens:* from the Latin *multus*, meaning many, and *dens* (masculine) meaning teeth.

Locality: West side of Puerco River opposite El Rito, New Mexico.

Horizon: Abo Formation, Lower Permian.

Collector: Paul C. Miller.

Diagnosis: Same as for genus.

Referred specimen: UCMP 40103, skull.

Locality: Camp quarry V-2814, one mile southeast of Arroyo de Agua, New Mexico.

Horizon: Abo Formation, Lower Permian.

Discussion: From re-examination of the type of *Aspidosaurus novomexicanus* it is evident that the two specimens that have been referred to that species belong to a distinct genus and species. In both CNHM 673 and UCMP 40103 there is room for 70 or more teeth in each jaw, while in the *A. novomexicanus* type the tooth size of the one or two teeth present indicates that there would be room for only 45-55 teeth. Differences in the armor are also distinctive. In *Aspidosaurus novomexicanus* none of the shields are fused to the expanded neural spines. Only seven shields are preserved, none of which is in contact with the others, and the first and seventh are longer than the remainder. In the Chicago Museum specimen, the anterior, although not the posterior, shields are fused to the neural spines, and all the shields are in contact with the preceding and succeeding plates. The total number of shields is not known, but it certainly exceeds seven, and all of the shields are of approximately the same size. The University of California specimen has no postcranial material.

As was pointed out by Langston, the general configuration of the skulls and particularly the pattern of ornamentation of the specimens that have been referred to *Aspidosaurus novomexicanus* are very similar to those of *Broiliellus*. There are, however, other features of the skull and particularly of the armor which separate the two groups. Three features differentiate the California and Chicago skulls from *Broiliellus brevis* and *B. texensis*. The former have a great many more teeth, the pattern of ridges is more subdued, and there is a median rostral fontanel. The width of the armor is on the order of that observed in *Broiliellus brevis*. The armor differs, however, not only in the fusion of the anterior plates, but also in the shape of the individual shields — relatively flat in *B. brevis*, and in the shape of an inverted V in these specimens.

Both specimens of *Conjunctio multidens* were collected from the Abo Formation near Arroyo de Agua. According to Romer, the Abo is roughly equivalent to the Putnam Formation, perhaps including the upper portion of the Moran and the lower Admiral. Their stratigraphic position as well as their morphology suggests derivation from *B. brevis* or a closely related predecessor. They clearly represent a different line of development from that expressed by *Broiliellus brevis* and *B. texensis*, and so should be placed in a separate genus.

CONJUNCTIO sp.

Figure 19

A third specimen (MCZ 2369) obviously referable to *Conjunctio* has been found in the Admiral Formation of Texas. It was collected by Dr. Romer in 1950 from the Halsell Hill locality, Section 19, Halsell subdivision, Clay County, Texas. Like the New Mexico specimens, it has a large number of teeth, a median rostral fontanel and a similar pattern of armor. No specific features separate it from the other members of the genus, except its place of discovery. This, however, is itself quite significant since the Texas and New Mexico land areas were separated during the Permian by a long arm of the sea, and only one vertebrate species, *Zatrachys serratus*, has been reported in both areas (Langston, 1953). For this reason I hesitate to place this specimen in the same species as the New Mexico specimens, despite their morphological similarities. All three specimens are of about the same geologic age.

The specimen includes the skull and fragments of both lower jaws, about 14 vertebrae with ribs and armor, portions of the shoulder girdle and front limbs. The skull roof is almost complete, lacking only the right front margin, the back of the skull table and the rear portion of the upper jaws on both sides. The skull has been greatly flattened, particularly in the antorbital region, distorting somewhat the outline of the skull. If restored to its original shape it would resemble closely the skull described by Langston which I refer to *Conjunctio multidens*. The portion of the skull posterior to the orbits is relatively short, as in other dissorophids from the lower part of the Wichita. The right tabular is intact and there is no bar closing the otic notch. The pattern of ornamentation is the same as in other members of this genus. The jugal overlaps the quadratojugal and maxilla as in *Broiliellus brevis*. A scrap of bone is present in the left orbit, presumably representing the remnant of a supraorbital plate. There is a suggestion of sclerotic plates in the same orbit. Since sclerotic plates are present in the Pennsylvanian dissorophids, they presumably existed in all of the Permian members of the family as well.

Most of the suture lines are visible, or can be readily restored by comparison of the two sides of the skull. The configuration of the individual bones differs from that of *Broiliellus* or *Tersomius* only in the greater length of the nasals as compared with the frontals. This, of course, is accentuated by the flattening of the forepart of the skull. The median rostral fontanel is in the same position as is the internarial bone in *Tersomius*, and of about the same size. The left lower jaw is fortunately displaced inward, allowing all of the teeth in the upper jaw to be visible. In spite of a short gap in the tooth row in the maxilla, there are 48 teeth, with room for 16 more, not counting the gap which could have accommodated about 6. The premaxilla has 10 teeth, with room for 6 more. The teeth are considerably larger in the premaxilla and anterior portion of the maxilla than they are in the posterior region of the upper jaw. All of them are broken off, but would probably have been a millimeter or two in length. The jaw fragments are too incomplete to describe.

Two small blocks of matrix containing a number of vertebrae, ribs and armor were found together with the skull. The bones are broken and jumbled in a very hard matrix, so few details are visible. The atlas and axis are not present and other anterior vertebrae may also be missing. The neural spines of the first two anterior vertebrae preserved are truncated and the armor is lost. The 3rd through 9th vertebrae have fused armor plates. In the second block of matrix, probably contiguous with the first, the first vertebra is truncated dorsally while the second has a fused armor plate. If it is assumed that only the atlas and axis are missing from the anterior block, the first 13 vertebrae have fused armor plates. The neural spine of the 14th vertebra is complete and lacks fused armor. A free armor plate lies close to this vertebra, but could equally well have come from further on down the column. The 15th and 16th vertebrae have broken neural spines; no others are present in the block. Only the single free plate was found.

None of the fused plates are complete; all have been broken on the margins. Each had been about 5 mm long, and perhaps 10 mm wide. The sides meet at an angle of about 135°. On the dorsal surface, immediately above the neural spine, the armor is not sculptured. The sides, however, are deeply pitted.

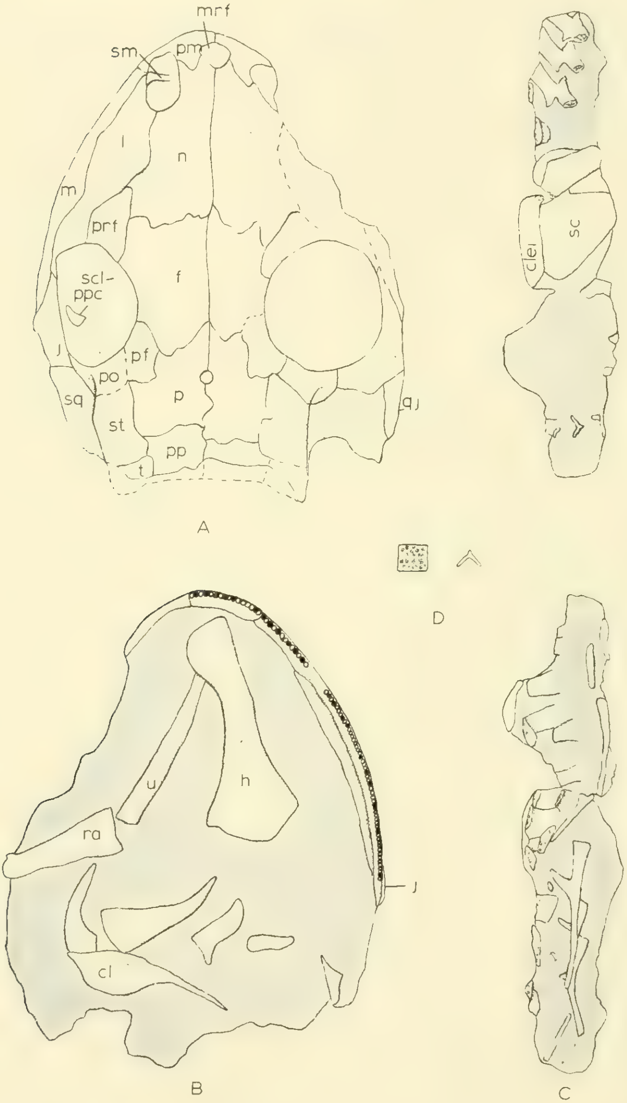

mrf
sm
pm
l
n
m
prf
scl-
ppc
f
j
pf
po
sq
p
st
pp
t
qj
A
clei
sc
D
h
u
ra
j
cl
B
C

FIG. 19. *Conjunctio* sp. MCZ 2369. A, Dorsal view of skull; B, Ventral view of skull; C, Right and left views of blocks containing postcranial material; D, Detail of free armor plate in dorsal and anterior views. × 3/4.

The single piece of free armor is well preserved. Again it is in the shape of an inverted V, the sides meeting at an angle of about 100°. Each side is about 3 mm wide and 5 mm long. An unsculptured ridge runs along the line of juncture of the sides which are sculptured with prominent pits except for a narrow strip on each margin. In contrast to *C. multidens* there does not appear to have been any ventral projection from the armor plate. There is no evidence of a second layer of armor.

The vertebrae themselves are poorly preserved; none of the central elements are visible. The anterior neural arches bear large transverse processes, similar to those of other dissorophids. The neural spines are expanded laterally beneath the armor to a lesser extent than in *Aspidosaurus novomexicanus*. Those beneath the fused plates are elongated anteroposteriorly, with the neural spines of the 7th and 8th vertebrae appearing to be in contact. Other vertebrae are not well enough preserved to determine the extent of their neural spines.

A number of ribs are preserved, those in the anterior portion of the block bearing prominent uncinate processes. None of the ribs are sufficiently complete to give dimensions.

Undiagnostic fragments of the right scapula and cleithrum are present along the vertebral column. Humerus, clavicle, radius, ulna, and scraps of other limb bones are present between the lower jaws. All are either too incomplete or distorted to give any description. Their size and general configuration indicate that they probably belong with the skull.

Interrelationships of the Permian Dissorophids

Tersomius texensis, although the most primitive of Permian dissorophids, is not a likely ancestor for the remainder of the group. It has at least two specializations not found in any later dissorophids: the possession of a second pair of vomerine teeth, and the presence of an internarial bone. The earliest specimen of *Tersomius*, MCZ 1911, from the Pueblo-Moran boundary, may lack these peculiarities, but distortion in the nasal region prevents definite determination. In all probability the internarial bone was smaller than in the Putnam specimens, if not altogether missing. The second pair of vomerine teeth is not visible, but these are small in other specimens of *Tersomius*, and may easily have been overlooked and removed during preparation. The other characters of this skull correspond to those of other specimens of *Tersomius*. Evidently there existed in the Pueblo or perhaps in the late Pennsylvanian a species of *Tersomius* lacking the specializations of *T. texensis*, which gave rise to the dissorophid genera with ornamented skulls.

The changes between *Tersomius* and *Brevidorsum*, the earliest ornamented genus, are relatively slight, at least in cranial anatomy. The skull roof behind the orbits becomes elongated relative to the length of the jaw suspensorium so that the end of the quadrate lies even with the end of the tabular, the angle between the skull table and the cheek region becomes sharper, the distance between the orbit and the otic notch becomes shorter, and the skull begins to show signs of ornamentation. Since the palate is not well preserved in the single specimen of *Brevidorsum*, it is impossible to tell whether the sutural basicranial articulation possessed by later dissorophids was developed.

Brevidorsum appears to have been ancestral to *Broiliellus* and *Dissorophus*. The simple nature of the armor in *Broiliellus* suggests that that genus evolved first, and that secondary elaboration has produced the pattern of armor seen in *Dissorophus*. Skull changes between *Brevidorsum* and *Broiliellus* are restricted to development of ornamentation and reduction in the depth of the back of the skull table. Lack of postcranial material in *Brevidorsum* precludes determination of the time during which armor first appeared.

Dissorophus and *Broiliellus* had definitely become differentiated from one another by the Putnam, although neither had developed all of its definitive characters by this time. It is apparent that *Broiliellus brevis*, *B. texensis*, and a third species from the Arroyo (being described by DeMar) represent successive stages in one line of evolution. Between the first two species the armor grew greatly in width, while throughout the series the skull developed more and more prominent ridges and tuberosities. *Dissorophus angustus* and *D. multicinctus* represent a similar line of evolution. Between these two species the armor increased greatly in width, and extended caudally to several additional segments, while the otic notch became closed posteriorly.

Conjunctio evidently arose from a species near the base of the *Broiliellus* line. It may have arisen either from *B. brevis*, or a closely related antecedent species. Not only have the anterior plates become fused, but additional plates have been added posteriorly and the shape of all of the armor has been altered. If there were any increase in the width of the individual plates, it was slight.

DeMar, on the basis of the armor, considered *Cacops* and *Alegeinosaurus* close to *Aspidosaurus*, and only distantly related to *Broiliellus* and *Dissorophus*. The discovery of *Broiliellus brevis* and *Dissorophus angustus*, as well as consideration of *Conjunctio*, reveals that neither the width of the armor nor its fusion serves to separate the two groups.

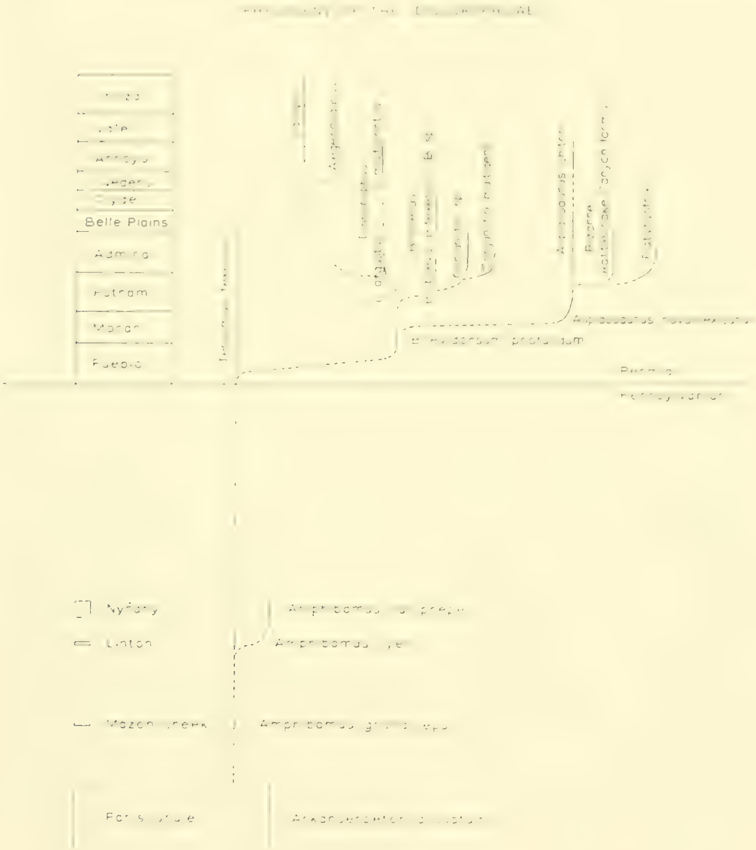


FIG. 20. Phylogeny of the Dissorophidae.

As was mentioned earlier, the pattern of armor in *Cacops* could have evolved simply by fusion of the ventral series of an animal with the pattern of *Dissorophus angustus*. Less likely would be the development of pitted, expanded neural spines beneath a single layer of armor from an animal with the pattern of *Broiliellus brevis.* The time gap between *Cacops* and the early species of *Broiliellus* and *Dissorophus* is certainly great enough to allow evolution of the characters that separate *Cacops* from the other genera, such as reduction in the number of presacral vertebrae and development of a second pair of sacral ribs. From the information now available, the most likely ancestor of *Cacops* would be a closely related predecessor of *Dissorophus angustus* in which there was no fusion of anterior armor plates, but in which the external series of armor had begun to develop. Both internal and external series must have then extended posteriorly, while the internal layer became fused to the neural spines, as did the anterior plates in *Conjunctio.* The posterior closure of the otic notch must have occurred independently in *Cacops* and *Dissorophus.* Evidently *Cacops* and *Alegeinosaurus* are closely related and so presumably diverged from one another a considerable length of time after the acquisition of a common pattern of armor.

If any form is to be separated from the remainder of the dissorophids on the basis of armor, it would be *Aspidosaurus,* since all species for which sufficient information is available have two or more sizes of armor on a single animal, a situation not known in any of the other dissorophids. The skull of *A. chiton* is unmistakably dissorophid in the possession of prominent otic notches and the pattern of cranial ridges described by Broili. However, the skull differs from that of all other dissorophids, with the exception of a genus being described by DeMar, in the great length of the face anterior to the orbits. The variation in the configuration of the armor along the vertebral column is particularly evident in the type of *A. chiton,* in which there is little question that all of the variants belong to the same animal. In *Aspidosaurus novomexicanus,* which is a much earlier species, the variation is not so striking, but the first and seventh shields are definitely larger than the remainder. Unfortunately, much of the armor which has been attributed to this genus was not found with other remains, and so definite association with this genus or even reference to the Dissorophidae in general is not always certain. The information now available suggests that there are probably a number of fairly closely related genera among the forms now called *Aspidosaurus.* These probably evolved from the remainder of the dissorophids early in the Permian or late in the Pennsylvanian. If *A. novomexicanus* is accepted as an early member of this group, it is probable that, as with the other dissorophids, the armor first developed as separate dermal ossifications situated dorsal to the neural spines, secondarily becoming fused. If this were the case, there may have been a common ancestor of both the *Aspidosaurus* group and the remainder of the dissorophids that had a small number of narrow, unfused armor plates above the anterior region of the vertebral column. It is at least possible that *Brevidorsum profundum* or a closely related predecessor had these characteristics.

In this discussion of phylogeny there has been no attempt to separate the evolutionary line that occurred in Texas from that developed in New Mexico. Such a separation is simply not possible with the limited number of genera known from New Mexico, and the limited time span of the New Mexico beds.

PENNSYLVANIAN DISSOROPHIDS

Since dissorophid remains are present in the very lowest beds of the Texas Permian, it is natural to look for their antecedents in the Pennsylvanian. Dissorophids have been described from Mazon Creek (Gregory, 1950), and members of this family have been mentioned from the fauna of Nýřany, Bohemia, and from the Paris shale of Kansas (Romer, 1947). The best preserved Pennsylvanian dissorophids, however, are from Linton, Ohio. Several specimens pertaining to members of this family have been discovered by Dr. Baird during his extensive preparation of that fauna. Because of the investing matrix, the early descriptions of this material were rather incomplete and led to the erection of a number of genera. It now appears that all of the dissorophid material from Linton belongs to a single genus and species. This species resembles *Amphibamus grandiceps* in many features, but is sufficiently different to be placed in a separate species as *Amphibamus lyelli*.

AMPHIBAMUS LYELLI (Wyman)

Figures 21-25; Plate 2

Raniceps lyelli Wyman, 1858, p. 168.
Pelion lyelli (Wyman), Cope, 1868, p. 221.
Tuditanus mordax Cope, 1874, p. 274.
Diceratosaurus punctolineatus, Moodie (not Cope, 1875), 1909, p. 25.
Diceratosaurus punctolineatus, Moodie (not Cope, 1875), 1916, p. 118.
Diceratosaurus brevirostris, Romer (not Cope, 1874), 1930, p. 91.
Platyrhinops mordax (Cope), Steen, 1931, p. 865.

Type: AMNH 6841, skull and complete skeleton.

Referred specimens: AMNH 2566, cranial fragments; BM (NH) R.2670, skull; USNM 4461, partial skeleton; MCZ 1277, lower jaws and palate.

Horizon and locality: Upper Allegheny. All from Linton, Ohio.

Revised diagnosis: Primitive dissorophid. No cranial ornamentation, pre- and postfrontals meeting above orbit. Seventy to eighty teeth in each jaw. No armor.

Description: The skull roof of the type specimen of *Amphibamus lyelli* (Fig. 21 A) is nearly complete, although slightly disarticulated at the margins. It is flattened in the manner of all Linton material, with the skull roof forced almost into the plane of the palate. The only portion of the skull that is missing is that anterior to the external nares. The occipital region extends horizontally behind the skull table, but shows few details.

TABLE 3

Cranial Dimensions of *Amphibamus*

	Amphibamus lyelli			*Amphibamus callipreps*
	Type AMNH 6841	BM(NH)[1] R.2670	MCZ 1277	BM(NH)[1] R.2817
Length of cranium to extremity of quadrate	31	—	64	—
Length of cranium along midline	26	—	—	40
Greatest width of cranium between quadratojugals	32	57	56	51
Least width between orbits	8	19	—	14
Transverse diameter of orbits	10	—	—	—
Longitudinal diameter of orbits	9	14	—	—
Distance from center of orbit to quadrate	17	—	—	—
Distance from center of orbit to front of skull	14		—	—
Distance of pineal from back of skull roof	6	11	—	9
Back of orbit to front of otic notch	4	9	—	—

[1] Measurements taken from drawing of specimen.
Dimensions of specimens are to the nearest millimeter.

The displacement of the marginal bones, together with the general compression, renders exact determination of dimensions difficult. It is about half the size, in any linear dimension, of

MCZ 1277 and BM(NH) R.2670. The closure of the sutures and the high degree of ossification of the skeleton, however, indicate that this specimen was an essentially mature individual.

The general skull shape closely resembles that of *Tersomius*: large, closely-set orbits, deep otic notches and a roughly triangular outline. There can be no question of the supratemporal-tabular suture as there is in *A. grandiceps.* The tabulars are small bones extending beyond the posterior margin of the skull table, slightly disarticulated from the supratemporals. The postparietals are relatively larger than those in *A. grandiceps* but,

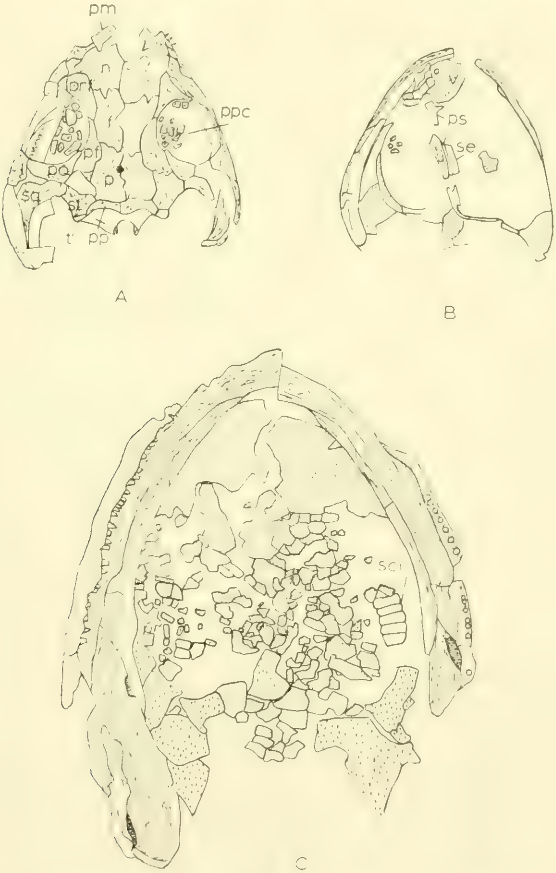


FIG. 21. *Amphibamus lyelli.* A, Skull roof, AMNH 6841; B, Palate, AMNH 6841; C, Palate, MCZ 1277. × 1.

like the tabulars, smaller than the corresponding units in *Tersomius*. The area of the skull table behind the orbits is shorter, relative to the total length of the skull, than that in Permian genera, but perhaps slightly longer than in *A. grandiceps*.

The bones ventral and anterior to the otic notch are displaced and partially obscured so that little can be said of them. The bones of the orbital margin differ from those of Permian dissorophids in that the pre- and postfrontals are in contact above the eye as they are in *A. grandiceps*. The jugals and lacrimals may make slight contact beneath the orbit, but this is not certain.

The medial bones of the skull roof differ little from those of other dissorophids except that the frontals do not enter the orbital margins. The pineal opening differs from that of the other species of dissorophids only in the better preservation which shows the presence of a circular ridge surrounding the opening. The anterior ends of the nasal bones are presumably lost along with the posterior margins of the premaxillae; at least, the adjacent margins of these bones cannot be made to match. Only the general position of the external nares can be determined. There is no sign of the septomaxillae. The front margins of the premaxillae can be determined by the position of the lower jaws. It is not possible to determine the presence or absence of an internarial bone.

The maxillae are both turned under the edge of the skull so that only their dorsal margins can be seen, together with portions visible through the orbits. Teeth are visible in side view in front of the right orbit; they will be described together with the palate.

Numerous pieces of sculptured bone are visible in both orbits. They are evidently remains of palpebral cups such as are present in *Tersomius*. Six sclerotic plates are visible beneath the left orbit, and two beneath the right in MCZ 1277. Presumably the animal had a ring of sclerotic plates similar to that described by Watson in *Amphibamus grandiceps*.

Like the type, the British Museum skull BM(NH) R.2670 has been subjected to crushing, which has disturbed the margins of the skull and forced the side walls into the same plane as the skull table. Restoration of these features produces a configuration very similar to that of the type, except for the greater distance between the orbits in BM(NH) R.2670. It is easy to interpret this difference as resulting from the larger size of this specimen. Fragments of the palpebral cups were noted by Steen in the same position as in the type.

The palate (Figs. 21 B and C) is similar in general to that of Permian dissorophids. Detailed structure is difficult to determine, however, since all of the specimens studied have a thick layer of denticulate "skin" covering most of the surface of the palate. The posterior region of the pterygoids can be seen in the British Museum specimen, with the exception of the basipterygoid articulation. This region is unfortunately obscure in the other specimens as well. The anterior portion of the pterygoid is also missing or obscure in all of the specimens. Enough of the vomer is visible in AMNH 2566, however, to indicate that the pterygoid did not reach that bone. Both ectopterygoids, each bearing one tooth, are present in BM(NH) R.2670, although somewhat disarticulated from the remainder of the palate. The relative position of the ectopterygoid can be judged in MCZ 1277 since the ectopterygoid tooth has penetrated the left lower jaw. The palatine bone and accompanying tooth can be seen only in AMNH 2566. Unfortunately, even in this specimen the posterior portion of this bone is missing and its relationship to the pterygoid can only be estimated. The palatine tooth is more laterally placed than its counterpart in Permian dissorophids.

The vomers are not completely visible in any single fossil, but from the several specimens their configuration can be determined. It is apparent that Steen's reconstruction of these bones places them too far posteriorly. In her specimen, the bones have either become disarticulated from the anterior margin of the skull, or the covering of denticulate "skin" has spread over the posterior margin making it appear that the bones extend into the interpterygoid vacuities. The relationship of the vomers can be seen in the type skull and in AMNH 2566. One pair of prominent vomerine teeth is situated just medial to the anterior margin of the internal nares, but there is no sign of the second pair noted in *Tersomius*. The anterior region of the vomers is covered by denticulate "skin" in all specimens; thus the presence or absence of an internarial pit cannot be determined definitely. An internarial pit has not been described in *A. grandiceps*. The configuration of the internal nares was determined from AMNH 2566. Their position is similar to that in *Tersomius*, although they are somewhat narrower. What were described by Steen as internal nares must have been only a rent in the palatal "skin" since their position in her reconstruction is much closer to the margin of the vomers than in any other dissorophid.

The parasphenoid is most readily observed in the British Museum specimen; unfortunately, it has separated from the pterygoids, and the adjacent margins of both bones are missing. Probably the relationship of the bones is similar to that observed in *Tersomius*, in which the parasphenoid overlaps the posterior margin of the basipterygoid process of the pterygoid, and the pterygoid and basisphenoid are in contact but have not completely fused. The position of the internal carotids is the same

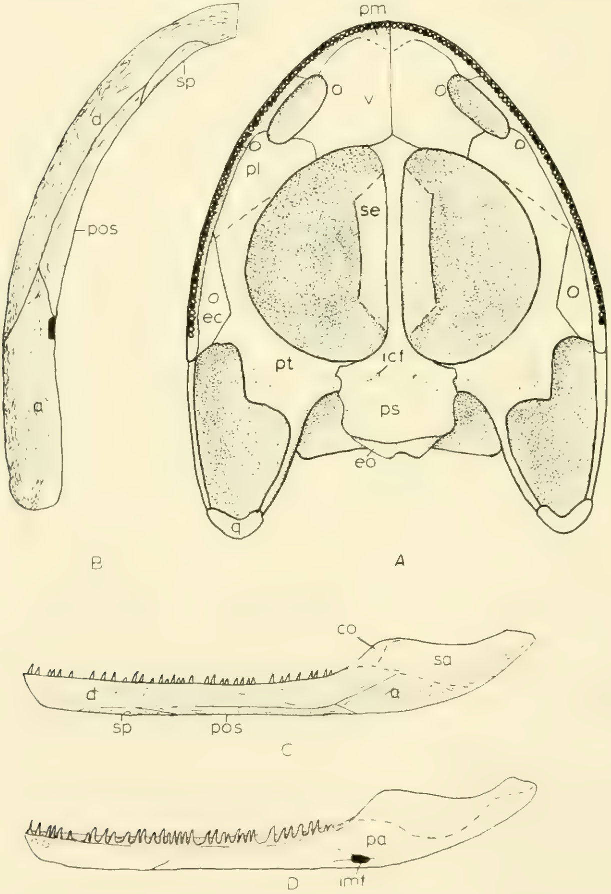


FIG. 22. *Amphibamus lyelli.* A, Restoration of palate; B, Restoration of lower jaw, based primarily on MCZ 1277, ventral view; C, Lateral view; D, Medial view. × 1.

as in *Tersomius.* The dorsal extensions of the parasphenoid plate lateral to the braincase, seen in Permian dissorophids, are not preserved in any of these specimens. The cultriform process is best viewed on the type. Its anterior extremity is expanded laterally where it is in contact with the vomers.

Marginal teeth are present in MCZ 1277, in the type, and in AMNH 2566. Although the entire complement is not present in any of these specimens, the number and density in all parts of the upper jaw can be determined. The number of teeth is approximately the same in all of the specimens regardless of the size of the skull. There is room for 21 in each premaxilla and 55 in each maxilla, compared with 13 and 34 respectively in *Tersomius.* They are the same size throughout the jaw; in the larger specimens they reach a length of about 2 mm. In the reconstruction (Fig. 22 A), the tooth replacement pattern in the right maxilla is based on MCZ 1277; the position of teeth and pits in the rest of the skull is arbitrary.

The quadrate is slightly visible in MCZ 1277, but the reconstruction is based primarily on other dissorophids.

Only in the type specimen is the sphenethmoid visible. Although incomplete, it apparently resembled that bone in other dissorophids. Except for the occipital region in the type, the posterior portion of the braincase is not visible in any of the specimens.

A layer of denticulate "skin" covered almost the entire palate in the living animal. Gaps were present for the reception of the palatine teeth, and in the region of the internal nares and adductor fenestrae, but most or all of the interpterygoid vacuities were covered. The denticles, particularly large in the region of the pterygoids, must have been of use in holding prey. It seems doubtful that such a thick layer of denticulate "skin" covered the palate in Permian dissorophids, which all have denticles growing from the bones themselves. It may, however, have covered the interpterygoid vacuities in these genera.

The reconstruction of the palate (Fig. 22 A) is probably accurate in the representation of individual units; however, one entire specimen might have somewhat different relative dimensions, since specimens of several sizes were used in making this reconstruction.

The lower jaws are restored primarily on the basis of MCZ 1277. The general configuration of the jaws can only be approximated since they were all somewhat crushed into the skull roof on the specimens studied. The only point of difference from the customary rhachitomous pattern is the apparent unity of the angular and surangular. Not only is there no suture separating them, but even in the pattern of dermal sculpture they appear as one. This is probably a result of the age of the specimen since it is the largest of all known Pennsylvanian dissorophids. This suture is also difficult to find in some specimens of *Tersomius*.

The features of the skull of *A. lyelli* generally resemble those of *Tersomius* and the other Permian dissorophids, except for the contact of the prefrontal and postfrontal above the orbit, and the greater density of marginal teeth (exceeded only by *Conjunctio*). The region of the skull roof posterior to the orbits is shorter relative to the anterior region of the skull than in advanced dissorophids, but similar to that of *Tersomius* and *Amphibamus grandiceps*.

The type specimen includes an almost complete skeleton, lacking only the tail and some of the fingers and toes. The specimen is preserved so that most of the right side is visible, with some features, however, present in a cast of the opposite side.

Supplementary information is provided by USNM 4461 (Fig. 24). This specimen unfortunately lacks the anterior end of the skeleton and the skull. Judging from the relative size of the skull and postcranial material of the type, this specimen must have had a skull about the size of MCZ 1277 or BM(NH) R.2670.

There are 25 presacral vertebrae in the type specimen. The exact number (if there is a fixed number) is in dispute in *A. grandiceps*. Watson (1940) and Gregory (1950) agree that CNHM 2000 has 18; Gregory notes 21 in the type of *Mazonerpeton*, which Moodie (1916) says has 27. The first two vertebrae are modified and might be called cervicals. The first lacks transverse processes and ribs, is much narrower than its fellows, and has special articulations with the occipital condyles and with the second vertebra. The exact nature of either of these articulations is uncertain. A single neural spine is visible; whether a second was present as in *Dissorophus* (Williston, 1910) cannot be determined. The spine is narrow, and appears slightly shorter than those of the remainder of the anterior vertebrae. The atlas does not overlap the second cervical to the extent seen in *Dissorophus*. The neural arch of the atlas is fused to the intercentrum. No separate pleurocentra are visible, and they too may be fused to the arch. No proatlas was seen.

The second vertebra has a short neural arch, small transverse processes, and no ribs. It articulates with the atlas by an ill-defined anterior extension above the neural canal. Its posterior zygapophyses are like those of the rest of the column. Between the second and third vertebrae there is a free intercentrum, but no pleurocentra are visible.

The 3rd vertebra is similar to numbers 5 through 25; the 4th, however, is modified in having a shorter neural spine, contributing as in *Eryops* to greater ease in lifting the head. Vertebrae numbers 3, and 5 through 25, are quite uniform and display the normal rhachitomous pattern. The neural spines are all short and unornamented. There is one sacral vertebra which bears a large sacral rib, as in *Eryops* and *Dissorophus*, but unlike the condition in *Cacops*. Five postsacral vertebrae are visible but are so badly crushed that just enough remains to show a general resemblance to the dorsals.

The position and general configuration of the intercentra and pleurocentra are visible in numerous vertebrae, but no thorough description is possible since they are always somewhat obscured by the remainder of the vertebrae, the ribs and matrix.

Ribs are present on all the vertebrae behind the cervicals. There may have been a small rib on the second vertebra, which bears a reduced transverse process, but none is visible. *Dissorophus angustus* has no rib in this position; the condition in *A. grandiceps* cannot be ascertained. The first three ribs are the longest (5 mm) and have widely expanded, overlapping ends. The fourth and fifth ribs are transitional, while the rest of the column bears ribs without distal expansions. Behind the shoulder region the ribs become shorter, having a length of only 3 mm just anterior to the sacrum. The ribs of the first two postsacral vertebrae are about this same length. The next two ribs are longer and the last visible one is very short. None was seen on the 32nd vertebra, but exact determination was difficult due to its crushed condition. The posterior ribs are much better preserved in USNM 4461 than they are in the type. Dorsally, presacral ribs 12 through 18 appear as straight rods, terminating in the tuberculum. Ventrally, the proximal half of the rod has a slender flange which terminates at the capitulum. The tuberculum and capitulum extend dorsally and ventrally from the body of the rib but apparently remain connected. Near the sacrum the ribs do not bear this ventral flange so that the two heads together form a greatly expanded portion at the immediately proximal end. The two heads are

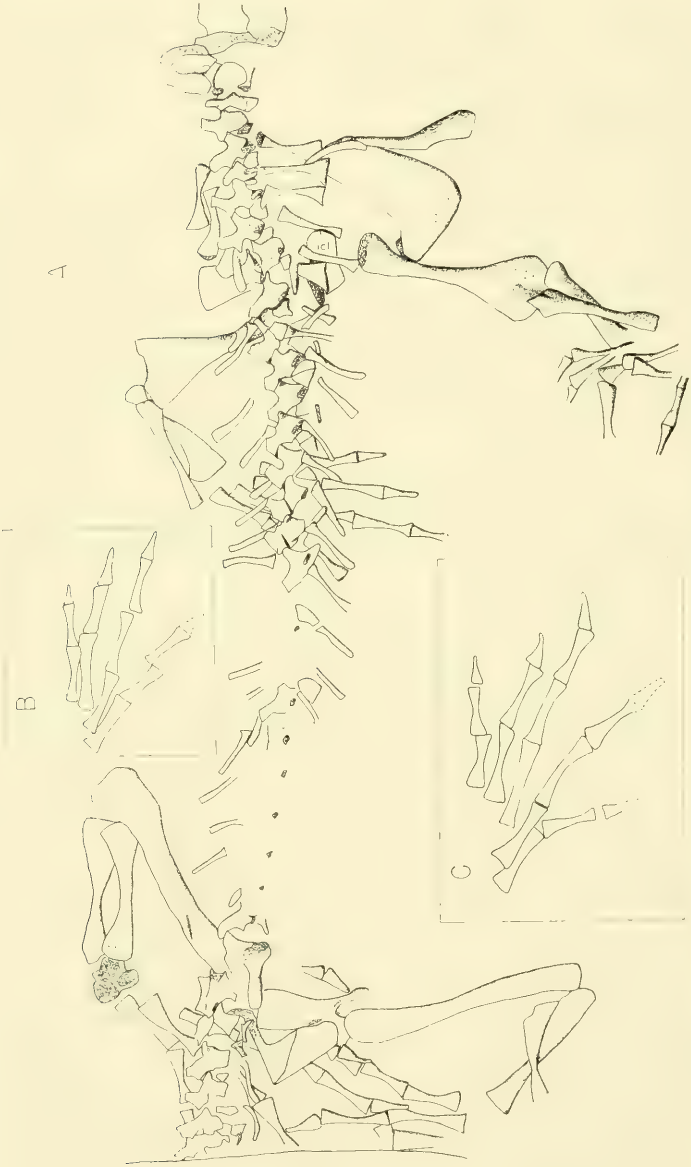


FIG. 23. *Amphibamus lyelli.* AMNH 6841. A, Skeleton; B, Manus; C, Pes. × 1½.

partially separated by a groove on the rear surface of the rib. The anterior surface is not visible.

The anterior ribs articulate with both the transverse process and the intercentrum, although the latter element does not have a particular area for its attachment as it does in *Cacops*. The ribs in the mid-portion of the column probably did not articulate with the intercentrum.

Both sacral ribs are preserved in the type; the left is visible from the medial surface affixed to the left ilium. The right is seen in lateral view, having partially separated from the right ilium. Each sacral rib includes a transverse bar articulating with a large transverse process of the sacral vertebra. This bar bends sharply caudad after contact is made with the ilium. It is not possible to determine the exact extent of the blade of the rib. The right appears similar to that of *Broiliellus brevis*, while the left appears more extensive, similar to that of *Dissorophus multicinctus*. Neither of the adjacent ribs is at all involved in the sacrum.

The pectoral girdle is essentially complete, although somewhat disarticulated. Its structure conforms to the general rhachitomous pattern. The scapulocoracoid plate is complete except for the glenoid region, which is obscured by the humerus. It is proportionately wider (or shorter) than that of *Eryops*. The scapulocoracoid plate compares very well with that of *Amphibamus grandiceps*. The cleithrum, as in that species, is restricted to the upper margin of the front of the scapula; there is little dorsal expansion, such as is visible in *Eryops*, and the stem is quite short. The stem of the clavicle extends further dorsally than it does in *Eryops*. The ornamented ventral extension of the clavicle articulates with the interclavicle. The latter bone can be seen only in dorsal view, partially concealed beneath the left coracoid. Its exact nature cannot be determined, but apparently it was similar to the interclavicle of *Amphibamus grandiceps*. The left scapulocoracoid can be seen from the inside, but it is covered by the vertebral column so that no details are visible. The position of the pectoral girdle along the vertebral column shown in Figure 25 is only approximate, based on the condition in *Eryops* and *Cacops*.

The humerus is longer, relative to the length of the vertebral column, than in either *Eryops* or *A. grandiceps*, having a considerable shaft between ends expanded at right angles to each other. The ectepicondyle and entepicondyle are visible on either side of the ulnar articulation. The position of the limbs prevents checking the presence of the pectoral process which was noted in *A. grandiceps* by Gregory. The limbs are turned so that the proximal expansion can only be seen on edge, hence its extent cannot be stated.

The ulna and radius are considerably shorter than the humerus. The ulna is best preserved on the right side; it is in place and the olecranon extends around the end of the humerus as a triangular process. The radius is slightly shorter than the ulna and expanded distally.

There are no ossifications in the region of the carpals.

All four digits of the left manus are well preserved, lacking only the distal phalanx of the lateral digit. The metacarpals are about one-half the length of the radius; the medial is the shortest and the next to medial, the longest. The proximal phalanges are about the length of the metacarpals; the distal ones are half that size and bluntly pointed. From the proportions of the remainder of the hand, one and only one phalanx can be added to the last digit. The phalangeal count is the same as in *A. grandiceps*: 2, 2, 3, 3. As in *A. grandiceps*, the third digit is the longest — somewhat longer than the humerus. The length of the digits and their compact form in the fossil suggests that webbing may have been present.

The dorsal portion of the pelvic girdle is clearly exposed. The lateral surface of the right half is visible, while the left shows its medial surface, partially covered by the right. As well as can be judged, each half is completely ossified, with no sign of sutures separating the individual bones. The most striking feature of the pelvis is the height of the ilium — quite similar to that of *Eryops*. On the lower portion of the posterior margin there is an indentation, below which is the ischium. Above this notch is a rugosity for a large muscle insertion. A small elevation is visible in this area in *Eryops*, and a large rugosity in *Dissorophus*. The ischium extends a considerable distance posteriorly. The puboischiadic plate is mostly missing and with it the bottom of the acetabulum and the ischiadic prominence. A well ossified pubis extends anteriorly. The anterior margin of the acetabulum is similar to that of *Eryops*. Dorsally there is a large central recess, the supra-acetabular notch. In general, the pelvis resembles that of *Eryops* more than it does the later dissorophids.

The pelvis of USNM 4461 is essentially the same shape as that of the type, again lacking the bottom of the puboischiadic plate. Enough of this is present, however, to indicate the presence of a small ischiadic prominence almost directly beneath the supra-acetabular prominence. The latter has the same position and configuration as it does in the type. The ilium differs from that of the type in being relatively shorter. The ischium is apparently broken at the rear.

FIG. 24. *Amphibamus lyelli.* USNM 4461. × 1.

Neither of the femora in the type is well preserved and both are turned at angles, obscuring the features most suitable for comparison with other dissorophids. Their most notable characteristic is their great length and lack of girth. The left femur is exposed in dorsal view, and both ends are crushed, obscuring any possible definitive features. From the rear an adductor crest is visible, but not sufficiently for description. The right femur can be seen in ventral view, showing a narrow adductor crest on the anterior, proximal margin. Both the proximal and distal ends are expanded, less so than in the Permian dissorophids, but with the same general configuration.

The femur of USNM 4461 is preserved in rear view, allowing observation of the adductor crest not possible in the type. The crest is restricted to the proximal half of the bone. It expands from the middle to within a millimeter or so of the proximal end, at which point it descends toward the articular surface. The dorsal surface of the femur is more concave, as viewed laterally, than that of any later dissorophids. There is an obvious surface for articulation with the fibula. The dorsal depression and the shape of the adductor crest are very similar to those observed in *Arkanserpeton.*

The fibula of the type is thinner and just slightly longer than the tibia. In *Eryops* the tibia is markedly longer, in *Cacops* slightly longer. The proximal expansions of the bones are about equal, while the distal expansion of the tibia is slightly larger than that of the fibula. The tarsals consist of five patches of cartilage.

The foot can be almost completely reconstructed from AMNH 6841. Of the five digits, only the distal phalanges of the lateral two are missing. The metatarsals are about one-half the length of the tibia; the medial one is the shortest; the remainder are all of approximately the same length. The proximal phalanges are all about the length of their metatarsals. The distal phalanges, like those of the hand, are half the length of the proximals and bluntly pointed. The second and third digits are the longest, both exceeding the length of the femur. As in the hand, webbing seems probable. The phalangeal count is: 2, 2, 3, 3, 3.

Habits: The general configuration of the skeleton indicates an active animal. Ossification is complete except for the carpals and tarsals, and the limbs are long relative to the length of the body. The lack of prominent tuberosities on the limbs, expected in an animal of small size, indicates that even the largest of these animals was not heavily built. An interesting feature is the length of the hands and feet, much in excess of those of any Permian dissorophids. Apparently this was an adaptation for a coal swamp environment. Little modification in this regard is noted in other portions of the animal's anatomy, however. The great length of the limbs, absence of lateral line canals, and the lack of a highly developed dermal shoulder girdle — associated in other forms with aquatic existence (Watson, 1919) — suggests that *Amphibamus lyelli* did not habitually

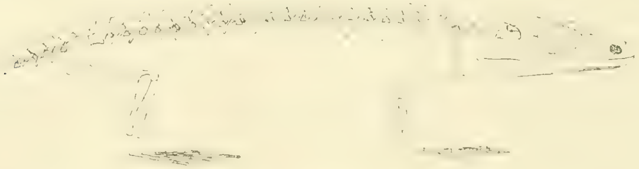


FIG. 25. *Amphibamus lyelli.* Restoration of skeleton. × 2/3.

live in the water. Supporting this is the almost complete ossification of the skeleton and the very well developed sacral attachment. The long, and perhaps webbed, feet would have allowed it to traverse readily bogs and shallow pools. As a response to increased aridity, its Permian descendants completely lost this adaptation.

AMPHIBAMUS CALLIPREPES (Steen)

Mordex calliprepes Steen, 1938, p. 260.

I have not been able to investigate personally any of the Nýřany material of possible dissorophid affinities. Nevertheless, the additional knowledge we now have concerning other Pennsylvanian species makes it necessary to comment further on those previously described. Three forms from Nýřany were considered by Gregory (1950) to be dissorophids. One is *Ricnodon limnophyes.* It is very difficult to conceive of this animal as even a member of the Rhachitomi, much less of the Dissorophidae. The structure of the palate is particularly difficult to reconcile. The shapes of the parasphenoid and pterygoids are vastly different from those of any dissorophid. The pterygoid, ectopterygoid and palatine all bear numerous large teeth not encountered in dissorophids. The orbits are separated by far too great a distance relative to their size for any known dissorophid, the pattern of sculpturing is different from that of any members of that family, and the tabular-supratemporal appears as a single bone rather than as separate units. Romer (1950) placed *Ricnodon* among the lepospondyls.

Gregory's inclusion of *Mordex calliprepes* (Steen, 1938) among the dissorophids is entirely justified. In fact, there is very little to separate this species from *Amphibamus lyelli* on the evidence of the skull roof and palate. The specimen on which this species is based is just slightly smaller than the British Museum specimen of *A. lyelli,* so comparison will be made with that form. The differences are primarily in proportion. In "*Mordex,*" the width across the back of the skull table is small compared with the length of the skull, the contact of pre- and postfrontal is larger than in *A. lyelli,* and the postparietals are narrower. When comparison is extended to the type of *A. lyelli,* it becomes apparent that the dimensions of "*Mordex*" are probably within the range of variation of that species. All the proportional differences, however, suggest a position slightly closer to *A. grandiceps.* For this reason, as well as the geographical separation of this form, it seems reasonable to maintain it as a distinct species, at least until more is known of the anatomy. There is one additional point of distinction. According to Steen (1938, p. 260), "there is a small pentagonal interfrontal bone present, which, unlike the other dermal bones, is unornamented." It seems possible that this may be only an artifact, especially since it is unsculptured.

Romer (1947) suggested *"Mordex"* as a possible ancestor of the trematopsids. While there is nothing to definitely bar it from such a position, it is certainly no closer to that family than any of the other Pennsylvanian dissorophids. It also has a large number of features that separate it from the known Permian trematopsids. The frontals do not extend in front of the orbits to the extent that they do in the Trematopsidae. The skull is not elongated in front of the orbits. The postparietals are quite small, as is the rear skull table. There is no apparent modification of the external nares.

Another form mentioned by Gregory as a dissorophid is a specimen of *Limnerpeton laticeps* (Fritsch, 1883, plate 36, fig. 1). The immaturity of the specimen prevents any conclusive statement.

AMPHIBAMUS GRANDICEPS Cope

This species was discussed quite thoroughly by Watson (1940) and by Gregory (1950), but in light of the evidence reported here, it is profitable to review certain features of its anatomy. The most important thing to keep in mind concerning the species is the small size and youth of all known specimens. The skull has many features peculiar to young individuals. Among these are the large size of the orbits, pineal foramen, and external nares, the tendency of the bones to separate, and the simplicity of suture lines.

One peculiarity that is not explained in this way is the lack of a suture between the supratemporal and the tabular. Apparently this is lacking on both of the extant specimens. Descriptions of two missing specimens, however, do indicate such a suture (Moodie, 1916, p. 128, fig. 26; and Hay, 1900, p. 122). It is almost certain from phylogenetic considerations that the tabular must have been a separate unit as it is in most of the Rhachitomi.

On two other points, changes might be made in recent descriptions. In the neotype, contrary to Gregory's interpretation, the jugal and lacrimal do appear to meet beneath the orbit, even if only with a very small contact. In Watson's description of the Chicago specimen he mentioned the existence of a patch of scale-covered skin which lay between the upper and lower jaws on the left side of the skull in about the same area as an orbit. He dismissed the idea that this was an ossification in the upper eyelid. In view of the condition in *Amphibamus lyelli* and particularly in *Tersomius*, it appears that this is just what it is, rather than part of a covering between the lower jaws.

Some of the features reported in earlier descriptions of *Amphibamus grandiceps* would separate it distinctly from *Amphibamus lyelli*. Several of these features were only inferred, however, and so may be ignored until they can be checked in more adequately preserved material. Whether there are ribs on the first, second and third vertebrae, as well as ahead of and behind the sacral rib, cannot be determined. CNHM 2000, on which most of the details of Watson's description were based, consists of molds of both sides of the bones, with the bone itself preserved only as a white film which has for the most part been removed. In preservation of this kind it is difficult to tell sutures from cracks, and irregularities in the matrix from features of the skull. There is nothing in either this skull or YPM 794 to determine the existence of the peculiar upper jaw joint described by Watson, or the unusual septomaxilla. A row of palatal teeth such as reported by Watson would be a decidedly unusual character for a dissorophid, and apparently consists of bases of teeth from the broken upper jaw, the ends of these teeth having remained in place in the maxilla to be preserved alongside their own roots.

As Watson stated, there is no sign of paired teeth on the vomers, palatines and ectopterygoids; they are apparently covered either by the lower jaws or by a layer of denticulate "skin" such as is present in *A. lyelli.* They may even be absent in such a young animal.

Despite the youth of these specimens, several features definitely distinguish them from *A. lyelli.* The number of marginal teeth is different in the two species but is relatively constant within the members of each. *A. grandiceps* has about 48 marginal teeth, while *A. lyelli* has about 76, regardless of the size of the skull. The number of presacral vertebrae appears to be less in *A. grandiceps,* but there is such a disparity in published counts for that species that no definite statement can be made. There are also changes in relative dimensions that may hold true for adult specimens of *A. grandiceps*. The pre- and postfrontals have a broader line of contact in that species than in *A. lyelli*, and the postparietals are smaller. A feature in which *A. grandiceps* differs from later dissorophids is the perforation of the stapes. In this species there is a definite hole near the base, while in *Broiliellus* and *Dissorophus* it is imperforate; the condition is not known in *A. lyelli* or in *Tersomius*.

ARKANSERPETON ARCUATUM Lane

An isolated femur was described by Lane (1932) from the Paris shale of Kansas, roughly equivalent to the McAlester shale, at the top of the Pottsville or the base of the Allegheny. He considered that it was an embolomere, but as Romer (1947) has pointed out, it is probably a dissorophid. It is larger than, although otherwise similar to, the femur of *Amphibamus lyelli*. None of the femora of Pennsylvanian dissorophids is well enough preserved to determine specific relationships.

INTERRELATIONSHIPS OF THE PENNSYLVANIAN DISSOROPHIDS

Compared with the Permian dissorophids, the Pennsylvanian members of the family are few and apparently little diversified. Despite the long time span during which dissorophids are known in the Pennsylvanian, there are at most two genera represented, compared with at least six genera in the Wichita group alone of the Lower Permian. This might be considered only a result of the general paucity of Pennsylvanian deposits were it not for the fact that the genus *Amphibamus* is known from three deposits of differing age and locality. This suggests that there was truly little diversity of the family in the Pennsylvanian.

The relationships among the three species of *Amphibamus* cannot be determined definitely, since *A. grandiceps* is represented only by very young specimens and *A. calliprepes* is known only from an incomplete skull table. All three may have developed from a common ancestor, or *A. grandiceps* may have given rise to the other two species. Nothing can be stated concerning the relationships of *Arkanserpeton* until more material is available.

Tersomius almost certainly evolved from *Amphibamus*, but it is not known from which species. It is probable that the remainder of the dissorophids evolved from *Tersomius* rather than directly from *Amphibamus* since *Tersomius* has several features of the higher dissorophids not yet acquired by *Amphibamus*, such as the entrance of the frontal into the margin of the orbit, a well developed internarial pit, and a reduced tooth count. It should be noted, however, that *Tersomius* shares most of its primitive features with *Amphibamus* and essentially represents a continuation of a line of evolution established in the early Pennsylvanian.

The critical point in the evolution of the Dissorophidae occurred when the group became armored. The unarmored genus *Tersomius* carried on throughout the Wichita group the general trends suggested by *Amphibamus* in the Pennsylvanian, but apparently did not produce any further lines of evolution after giving rise to the armored genera early in the Permian. The remainder of the family, in contrast, differentiated rapidly once armor became established.

RELATIONSHIPS OF THE DISSOROPHIDAE AMONG THE RHACHITOMI

The dissorophids can be traced back to the Middle or possibly Lower Allegheny. There is only one family to which the dissorophids are definitely known to be related — the Zatrachyidae. As was pointed out by Steen (1931), very few features separate *Stegops*, the earliest zatrachyid, from "*Platyrhinops*" = *Amphibamus lyelli*. Although some features appear to bar *Stegops* from a position of direct ancestry of the Permian zatrachyids (Langston, 1953), there is little doubt that this genus is closely related to the other members of the family.

All of the other families of the Eryopsoidea have been thought to be closely related to the dissorophids (Olson, 1941; Romer, 1947; and Moustafa, 1955), but as yet no forms have been described that are in any way intermediate between these families and the Dissorophidae. Nor can any direct relationships be found between any of the other rhachitomous groups and the dissorophids. As was pointed out by Romer (1947), most of the features of cranial anatomy point to a common origin for the Eryopsoidea. He did not, however, rule out the possibility that these features might have been achieved separately by the several families in that group.

Until more is known of early Pennsylvanian amphibians, it is not possible to determine either the ancestry or relationships of the earliest dissorophids.

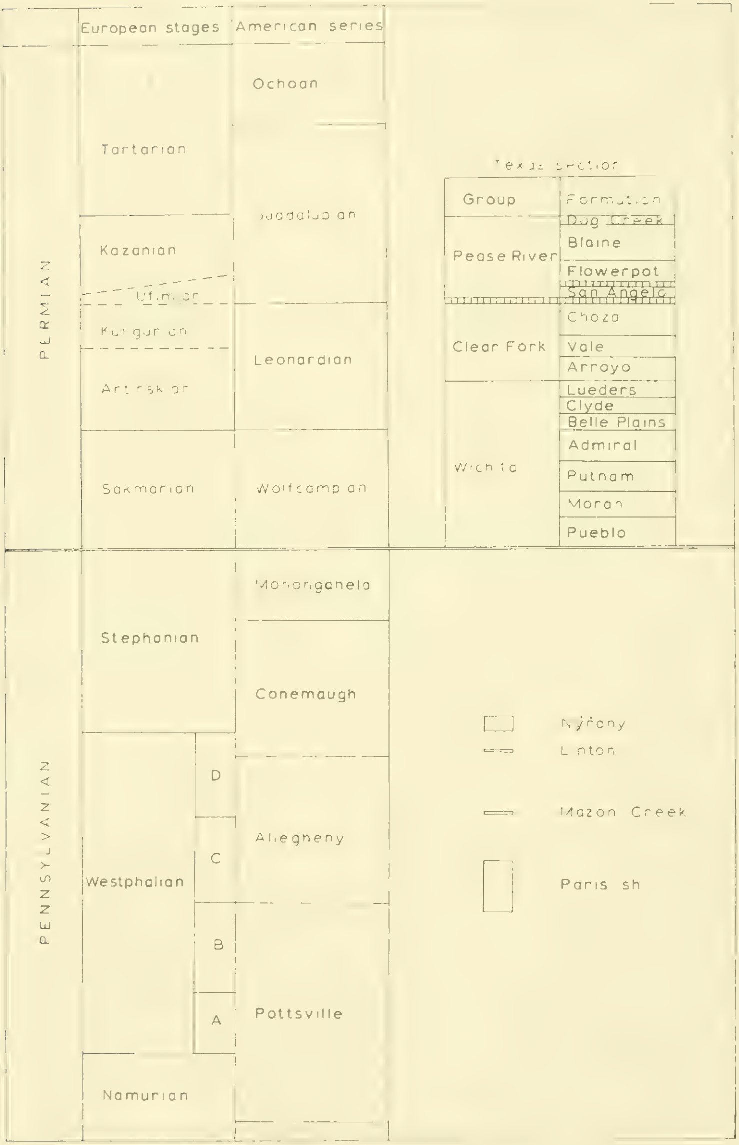

European stages
American series
PERMIAN
Ochoan
Tartarian
Guadalupian
Kazanian
Ufimian
Kungurian
Leonardian
Artinskian
Sakmarian
Wolfcampian
Texas section
Group
Formation
Dog Creek
Blaine
Pease River
Flowerpot
San Angelo
Choza
Clear Fork
Vale
Arroyo
Lueders
Clyde
Belle Plains
Admiral
Wichita
Putnam
Moran
Pueblo
PENNSYLVANIAN
Monongahela
Stephanian
Conemaugh
Nýřany
Linton
D
Mazon Creek
Allegheny
C
Westphalian
Parrish
B
A
Pottsville
Namurian

FIG. 26. Pennsylvanian and Permian stratigraphy. The chart is based primarily on Dunbar and others (1960), and Moore and others (1944). Correlation of localities follows Romer (1947 and 1958), and Panchen and Walker (1960).

ABBREVIATIONS

a	angular
ar	articular
asc	ascending process of epipterygoid
bo	position of basioccipital
bs	basisphenoid
cl	clavicle
clei	cleithrum
co	coronoid
co I	intercoronoid
co II	precoronoid
cof	coracoid foramen
d	dentary
e	epipterygoid
ec	ectopterygoid
eo	exoccipital
ext	armor, external series
f	frontal
fa	foramen for artery
fo	fenestra ovalis
fv	foramen for vein
gf	glenoid foramen
h	humerus
ic	intercentrum
icf	internal carotid foramen
icg	internal carotid groove
icl	interclavicle
icp	internal carotid passage
il	ilium
imf	inframeckelian fossa
ina	internasal
inp	internarial pit
int	armor, internal series
is	ischium
j	jugal
l	lacrimal
m	maxilla
mf	mandibular foramen
mrf	median rostral fontanel
n	nasal
nac	space for cartilaginous nasal capsule
nch	position of notochord
nl	nasolacrimal groove
o	otic capsule
obf	obturator foramen
p	parietal
pa	prearticular
pc	pleurocentrum
pf	postfrontal
pl	palatine
pm	premaxilla
po	postorbital
pos	postsplenial
pp	postparietal
ppc	palpebral cup
prf	prefrontal
pro	proötic process of epipterygoid
ps	parasphenoid
pt	pterygoid
ptf	posttemporal fossa
pu	pubis
q	quadrate
qj	quadratojugal
r	rib
ra	radius
rem	recess for rectus eye muscles
sa	surangular
sc	scapulocoracoid
scl	sclerotic plates
se	sphenethmoid
set	position of sella turcica
sgf	supraglenoid foramen
sm	septomaxilla
soc	supraoccipital
sp	splenial
sq	squamosal
sr	sacral rib
st	supratemporal
sta	supraorbital branch of stapedial artery
stp	stapes
t	tabular
u	ulna
v	vomer
vcl	vena capita lateralis
I-XII	foramina for cranial nerves

LITERATURE CITED

Broili, F.
1904. Permische Stegocephalen und Reptilien aus Texas. Palaeontographica, vol. **51**, pp. 1-49, 51-120.

Bystrow, A. P.
1935. Morphologische Untersuchungen der Deckknocken des Schädels der Wirbeltiere. 1. Mitteilung. Schädel der Stegocephalen. Acta Zool., vol. **16**, pp. 65-141.

Case, E. C.
1910. New and little known reptiles and amphibians from the Permian(?) of Texas. Bull. Amer. Mus. Nat. Hist., vol. **28**, pp. 163-181.
1911. Revision of the Amphibia and Pisces of the Permian of North America. Publ. Carnegie Inst. Washington, no. **146**, pp. 1-179.

Case, E. C., S. W. Williston, and M. G. Mehl
1913. Permo-Carboniferous vertebrates from New Mexico. Publ. Carnegie Inst. Washington, no. **181**, pp. 1-81.

Cope, E. D.
1868. Synopsis of the extinct Batrachia of North America. Proc. Acad. Nat. Sci. Philadelphia, 1868, pp. 208-221.
1874. Supplement to the extinct Batrachia and Reptilia of North America. I. Catalogue of the air-breathing Vertebrata from the Coal Measures of Linton, Ohio. Trans. Amer. Philos. Soc., vol. **15**, pp. 261-278.
1875. The extinct Batrachia of Ohio. Proc. Acad. Nat. Sci. Philadelphia, 1875, p. 16.
1895. A batrachian armadillo. Amer. Naturalist, vol. **29**, p. 998.

DeMar, R.
1961. A review of the family Dissorophidae (amphibians) with emphasis on the late Wichita and Clear Fork genera. Unpublished Ph.D. dissertation, Dept. of Geology, University of Chicago.

Dunbar, C. O., and others
1960. Correlation of the Permian formations of North America. Bull. Geol. Soc. Amer., vol. **71**, pp. 1763-1806.

Fritsch, A.
1883. Fauna der Gaskohle und der Kalksteine der Permformation Böhmens. 4 vols. Prague. (1879-1901.)

Gaupp, E.
1900. Das Chondrocranium von *Lacerta agilis*. Ein Beitrag zum Verständnis des Amniotenschädels. Anat. Hefte, vol. **15**, pp. 433-596.

Gregory, J. T.
1950. Tetrapods of the Pennsylvanian nodules from Mazon Creek, Illinois. Amer. Jour. Sci., vol. **248**, pp. 833-873.

Hay, O. P.
1900. Descriptions of some vertebrates of the Carboniferous age. Proc. Amer. Philos. Soc., vol. **39**, pp. 96-123.

Lane, H. H.

1932. A new stegocephalian from the Pennsylvanian of Arkansas. Kansas Univ. Sci. Bull., vol. **20**, pp. 313-317.

Langston, W.

1953. Permian amphibians from New Mexico. Univ. Calif. Publ. Geol. Sci., vol. **29**, no. 7, pp. 349-416.

Moodie, R. L.

1909. Carboniferous air-breathing vertebrates of the United States National Museum. Proc. U. S. Nat. Mus., vol. **37**, pp. 11-28.

1916. The Coal Measures Amphibia of North America. Publ. Carnegie Inst. Washington, no. **238**, pp. 1-222.

Moore, R. C., and others

1944. Correlation of Pennsylvanian formations of North America. Bull. Geol. Soc. Amer., vol. **55**, pp. 657-706.

Moustafa, Y. Shawki

1955. The affinities of *Parioxys ferricolus* and the phylogeny of the ''Eryopsoid'' amphibians. Bull. Inst. Egypte, vol. **36**, pp. 77-104.

Olson, E. C.

1941. The family Trematopsidae. Jour. Geol., vol. **49**, no. 2, pp. 149-176.

Panchen, A. L., and A. D. Walker

1960. British Coal Measure labyrinthodont localities. Ann. Mag. Nat. Hist., ser. 13, vol. **3**, no. 30, pp. 321-332.

Romer, A. S.

1930. The Pennsylvanian tetrapods of Linton, Ohio. Bull. Amer. Mus. Nat. Hist., vol. **59**, pp. 77-147.

1947. Review of the Labyrinthodontia. Bull. Mus. Comp. Zool., vol. **99**, pp. 1-368.

1950. The nature and relationships of the Paleozoic microsaurs. Amer. Jour. Sci., vol. **248**, pp. 628-654.

1958. The Texas Permian redbeds and their vertebrate fauna. *In:* Studies on fossil vertebrates, edited by T. S. Westoll. London, pp. 157-179.

Romer, A. S., and T. Edinger

1942. Endocranial casts and brains of living and fossil Amphibia. Jour. Comp. Neur., vol. **77**, no. 2, pp. 355-389.

Sawin, H. J.

1941. The cranial anatomy of *Eryops megacephalus.* Bull. Mus. Comp. Zool., vol. **86**, pp. 407-463.

Steen, M.

1931. The British Museum collection of Amphibia from the Middle Coal Measures of Linton, Ohio. Proc. Zool. Soc. London, 1930 (1931), pp. 849-891.

1938. On the fossil Amphibia from the Gas Coal of Nýřany and other deposits in Czechoslovakia. Proc. Zool. Soc. London, (B), vol. **108**, pp. 205-283.

SUSHKIN, P. P.

1927. On the modifications of the mandibular and hyoid arches and their relations to the braincase in the early Tetrapoda. Palaeont. Zeitschr., vol. **8**, pp. 263-321.

WATSON, D. M. S.

1919. The structure, evolution and origin of the Amphibia. — The "orders" Rachitomi and Stereospondyli. Philos. Trans. Roy. Soc. London, (B), vol. **209**, pp. 1-73.

1940. The origin of frogs. Trans. Roy. Soc. Edinburgh, vol. **60**, pp. 195-231.

WILLISTON, S. W.

1910. *Cacops, Desmospondylus:* new genera of Permian vertebrates. Bull. Geol. Soc. Amer., vol. **21**, pp. 249-284.

1911. American Permian vertebrates. Chicago, 145 pp.

1914. *Broiliellus,* a new genus of amphibians from the Permian of Texas. Jour. Geol., vol. **22**, pp. 49-56.

WYMAN, J.

1858. On some remains of batrachian reptiles discovered in the coal formation of Ohio, by Dr. J. S. Newberry and C. M. Wheatley. Amer. Jour. Sci., ser. 2, vol. **25**, pp. 158-163.

Received December 15, 1962.

PLATES

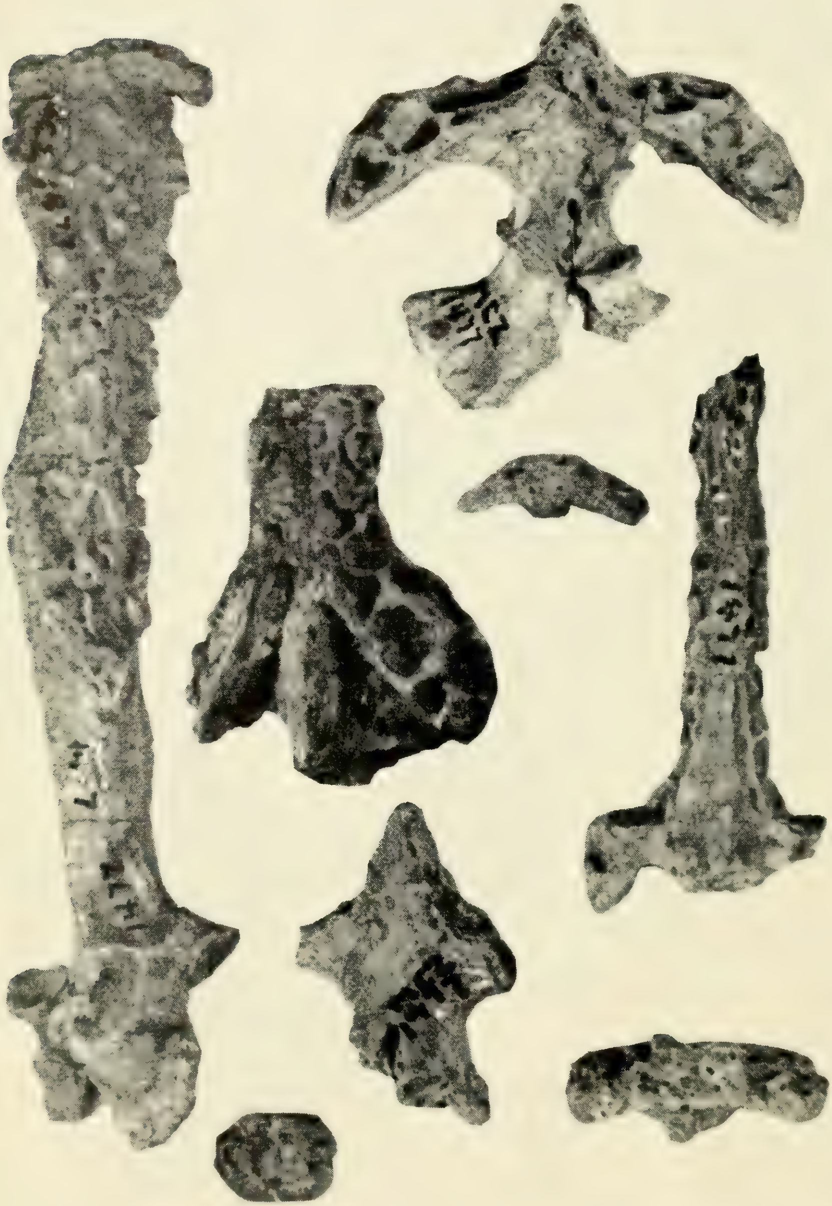


PLATE 1. Range of variation in "*Aspidosaurus*" armor. MCZ 1477, Rattlesnake Canyon, Admiral Formation. × 1.

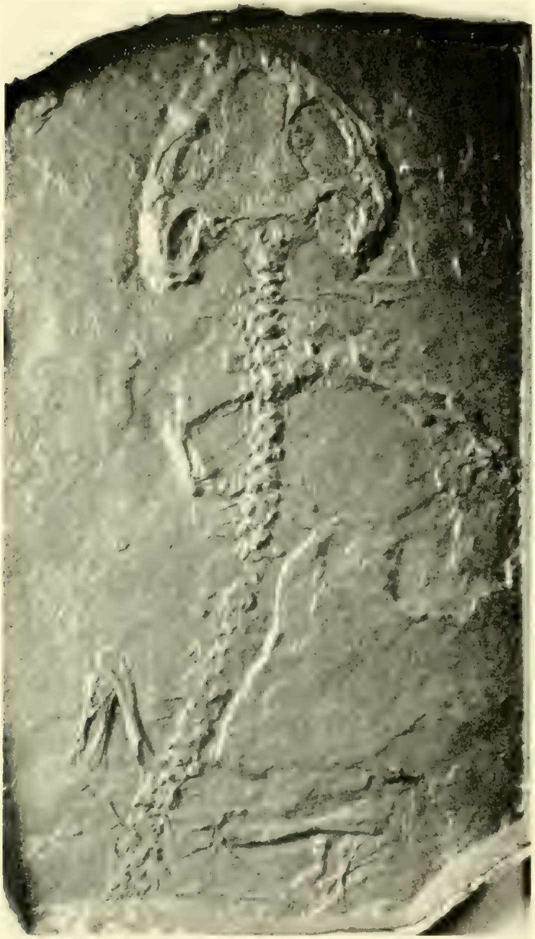


PLATE 2. *Amphibamus lyelli.* AMNH 6841, Linton, Ohio. × 1.

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 8

THE GENUS *MICRATHENA* (ARANEAE, ARANEIDAE) IN THE WEST INDIES

By Arthur M. Chickering

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
June 30, 1964

PUBLICATIONS ISSUED BY OR IN CONNECTION WITH THE

MUSEUM OF COMPARATIVE ZOOLOGY

HARVARD UNIVERSITY

BULLETIN (octavo) 1863 — The current volume is Vol. 131.

BREVIORA (octavo) 1952 — No. 204 is current.

MEMOIRS (quarto) 1864–1938 — Publication terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 41 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 28 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained from the Publications Office of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Peters' Check-List of Birds of the World. Volumes 1, 4 and 6 are out of print; volumes 2, 3, 5, 7, 9, 10 and 15 are currently available.

Phylogeny and Evolution of Crustacea. Proceedings of a conference held at Cambridge, Mass., March 6-8, 1962. H. B. Whittington and W. D. I. Rolfe, editors. Cambridge, Mass., 192 pp., 80 figs., 1963. Cloth bound, $6.75.

Fishes of the Gulf of Maine, by Henry B. Bigelow and William C. Schroeder. Washington, viii - 577 pp., 1953. Photo-offset reprint, $6.50.

PUBLICATIONS OF THE BOSTON SOCIETY OF NATURAL HISTORY

The remaining stock of the scientific periodicals of the Boston Society of Natural History has been transferred to the Museum of Comparative Zoology for distribution. Prices for individual numbers may be had upon request.

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 8

THE GENUS *MICRATHENA* (ARANEAE, ARANEIDAE) IN THE WEST INDIES

By Arthur M. Chickering

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
June, 1964

Bull. Mus. Comp. Zool., Harvard Univ., **131**(8):251-281, June, 1964

No. 8—*The Genus Micrathena (Araneae, Araneidae) in the West Indies*

By Arthur M. Chickering

In connection with my study of the genus *Micrathena* in Central America (1961) and South America (1960a, b, c), I have recently had the opportunity to study all specimens of the genus from the West Indies now in the collections of the Museum of Comparative Zoology at Harvard College. During the summer of 1958 I had the privilege of studying the West Indian specimens of *Micrathena* in the extensive collections of the British Museum (Natural History); the collections of the American Museum of Natural History have also been made available to me. As a result of my study I have found what I believe to be serious confusion in the identification of certain species native to the West Indies. It is also obvious that errors of synonymy have been made. I hope this paper will contribute to clarification of the difficulties.

I believe there is urgent need for some competent worker to study the whole genus for the entire Western Hemisphere with the intention of publishing a complete revision of the genus that would serve for many years, as Reimoser's (1917) work did for a generation. This extensive piece of work should be preceded by intensive collecting in the West Indies and, especially, in the tropical regions of South America. I am convinced that such field work would yield excellent results. Not only would new and interesting species be found but much progress could be made in the now difficult problem of correctly matching up the sexes.

Acknowledgments extended and appreciation expressed in recent published papers (Chickering, 1960a, b, c, and 1961) are here repeated with my personal gratitude for encouragement over many years. I also wish at this time to express my gratitude and appreciation to Dr. W. J. Gertsch, American Museum of Natural History, for the loan of a valuable collection.

Holotypes of *M. levii*, *M. gertschi*, and *M. praeterita* will be deposited in the American Museum of Natural History, New York City. Holotypes of all other new species will be deposited in the Museum of Comparative Zoology, Harvard University.

MICRATHENA Sundevall, 1833

Type species, *M. clypeata* (Walckenaer, 1806), designated by Simon, 1895:859.

Micrathena bryantae sp. nov.

Figures 1-3

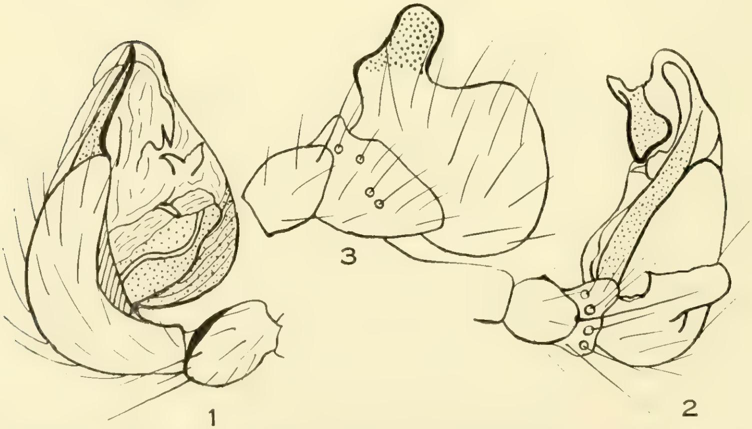
Note: Miss Bryant (1940) described briefly a single male from Cuba, but she did not give a specific name to it. I propose regarding it as the holotype of a new species and posthumously honoring its discoverer in its specific name.

Male holotype. Total length 4.4 mm. Carapace 1.76 mm long; 1.17 mm wide opposite posterior border of second coxae where it is widest; 0.59 mm tall at region of central fovea, which is a well marked circular pit; gently arched from PME to posterior declivity, with a pair of distinct dorsolateral foveae in the cephalothoracic groove.

Eyes. Ocular tubercles moderately well developed. Viewed from above, both eye rows moderately recurved; viewed from in front, anterior row gently recurved, posterior row definitely procurved, all measured from center. Central ocular quadrangle wider behind than in front in ratio of 21:19, slightly wider behind than long. Ratio of eyes AME:ALE:PME:PLE = 7:6.5:10:6 (long diameter used where differences exist). AME separated from one another by a little less than their diameter, from ALE by three times their diameter. PME separated from one another by about three-fifths of their diameter, from PLE by two and one-fifth

External Anatomy of *Micrathena*

Figures 1-3, *M. bryantae*



Figs. 1-2. Two views of the left palpal tarsus, tibia and patella.

Fig. 3. Nearly dorsal view of base of left palpal cymbium with basal tarsal hook, tibia and patella, more enlarged.

times their diameter. Laterals separated from one another by slightly less than one-third of the diameter of PLE. Height of clypeus equal to twelve-sevenths of the diameter of AME.

Chelicerae. Fairly robust; basal segment about 0.54 mm long; teeth along fang groove not observed because of fragility of the holotype.

Sternum. Scutiform in general; tubercles barely indicated; continued laterally between coxae and posteriorly between fourth coxae as slender sclerites; fourth coxae barely separated; surface very finely rugulose.

Legs. 4123. Width of first patella at "knee"[1] 0.16 mm, tibial index of first leg 11. Width of fourth patella at knee 0.15 mm, tibial index of fourth leg 11.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
I.	1.43	0.50	0.91	0.99	0.52	4.35
II.	1.37	0.49	0.78	0.85	0.48	3.97
III.	0.85	0.29	0.49	0.52	0.36	2.51
IV.	1.76	0.36	0.98	1.07	0.49	4.66
Palpus	0.33	0.12	0.15	——	0.66	1.26

Legs with few spines; these mostly broken off from handling. Hook on first coxa and corresponding ridge and groove on second femur lacking.

Palpus. See Miss Bryant's figure 143 (1940) for one view of the palpal tarsus and tibia, and Figures 1-3 in this paper for other views.

Abdomen. Length 2.73 mm; nearly rectangular in dorsal view (Miss Bryant's fig. 139); only moderately flattened; very little, if any, indication of suppressed spines.

Color in alcohol. See Miss Bryant's description (1940).

Type locality. The male holotype is from Cuba, Oriente, Los Llanos, 1000-2000 ft. elevation, July 16-20, 1936 (P. J. Darlington, Jr.).

Other records. A male in the American Museum of Natural History collected in Cuba, Soroa, Piñar del Rio, June 2, 1955 (A. F. Archer). This specimen was with an immature *M. forcipata* (Thorell), and a palpus from another male was found with females of *M. forcipata* (Thorell) taken in Cuba, Siboney, Oriente, November 17, 1945 (P. Olayo).

---

[1] The term "knee" is defined as the place of articulation of the patella with the femur; it is straight and easily measured. The term and its usage have been borrowed from Petrunkevitch's (1929, Trans. Connecticut Acad. Arts Sci., 30:11) method of deriving the tibial index. Tibial index is defined as width of patella × 100, divided by combined length of patella and tibia.

MICRATHENA CUBANA (Banks), 1909

Figures 4-10

Acrosoma cubana Banks, 1909. Juvenile holotype from San Diego de los Baños, Cuba, lost.

Micrathena cubana, Bryant, 1940; Roewer, 1942; Bonnet, 1957.

External Anatomy of *Micrathena*

Figures 4-10, *M. cubana*

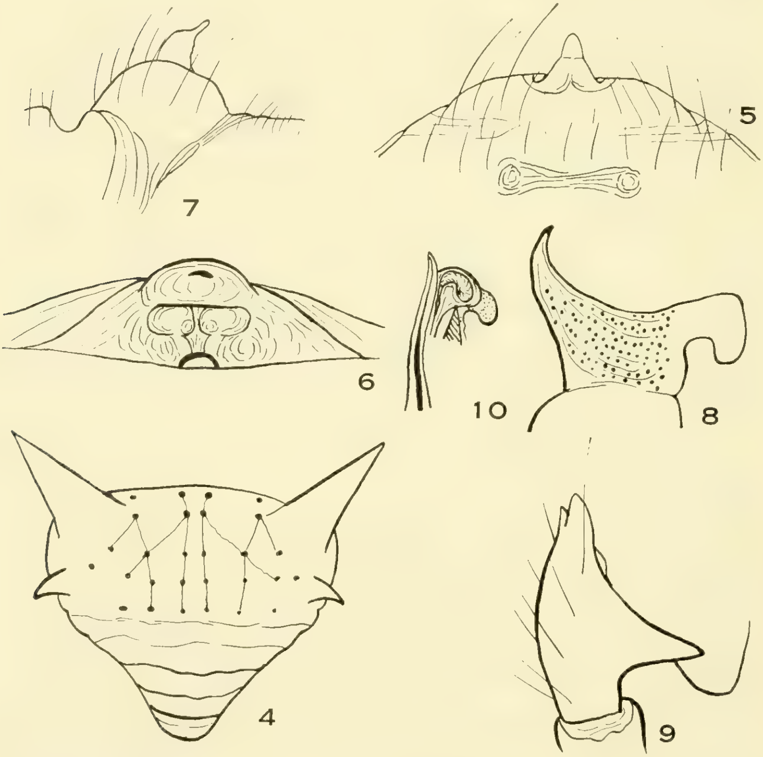


Fig. 4. Posterior end of female.

Figs. 5-7 Epigynum from below, in posterior view, and in profile, right side, respectively.

Fig. 8. Palpal tarsal hook of male.

Fig. 9. Palpal tibia of male to show characteristic form.

Fig. 10. Embolus and closely associated structures in male palpal tarsus, more enlarged.

Female. In addition to the abdominal spines described by Miss Bryant, there appear to be the remains of a reduced pair a short distance in front of the long, posterior pair. The appearance of the two pairs of posterior spines is shown in Figure 4. I see the epigynum as somewhat different from the figures accompanying Miss Bryant's description, and for that reason have provided Figures 5-7.

Male. Total length of the male 5.07 mm. Small remains of the two pairs of posterior spines show fairly clearly. Palpus: the basal tarsal hook is curiously developed (Fig. 8); the tibia also has a characteristic form (Fig. 9); the embolus and related structures are also more or less distinctive (Fig. 10). There is no ventral hook on the first coxa and, of course, the corresponding ridge and groove on the prolateral surface of the second femur are also lacking.

Collection records. With the possible exception of one specimen from the Dominican Republic, all of the numerous specimens examined are from Cuba; they are from many localities in this island. No males have been seen except those reported by Miss Bryant.

MICRATHENA FORCIPATA (Thorell), 1859
Figures 11-16

Acrosoma forcipatum Thorell, 1859. Female holotype from Cuba, in the Natural History Museum, Stockholm. Butler, 1873; Petrunkevitch, 1911; Bryant, 1940.

Acrosoma flavomaculata Keyserling, 1864. Female holotype from Haiti, in the British Museum (Nat. Hist.). Butler, 1873; Keyserling, 1892.

Micrathena flavomaculata, Simon, 1895; Petrunkevitch, 1911; Reimoser, 1917; Roewer, 1942; Bonnet, 1957.

Micrathena sexspinosa, Reimoser, 1917; Roewer, 1942; Bonnet, 1957. Not *M. sexspinosa* (Hahn).

During my visit to the British Museum (Natural History) in 1958 I had the opportunity to study Keyserling's types of *M. flavomaculata* and to make drawings of the epigynum and the abdomen. Since then I have been able to study several specimens of *M. forcipata* (Thorell) and I have been forced to conclude that *M. flavomaculata* and *forcipata* are the same species.

As Miss Bryant (1940) pointed out, Reimoser was clearly in error when he synonymized *M. forcipata* (Thorell) with *M. sexspinosa* (Hahn). Roewer (1942) and Bonnet (1957) have both followed Reimoser. There are very clear and definite differences between these two species in both sexes and there should be no further confusion regarding their separation.

Female. Total length of Keyserling's type of *M. flavomaculata* from base of chelicerae to posterior end of abdomen in midline, 8.97 mm; from base of chelicerae to opposite tips of large posterior spines, 11.5 mm. Corresponding measurements of a fairly typical specimen of *M. forcipata* (Thorell) from Cuba, 8.26 mm and 11.83 mm. The four typical pairs of spines are well shown in Miss Bryant's figure 149 but important variations have been noted; the anterior pair may be almost eliminated in certain specimens and

External Anatomy of *Micrathena*
Figures 11-16, *M. forcipata*

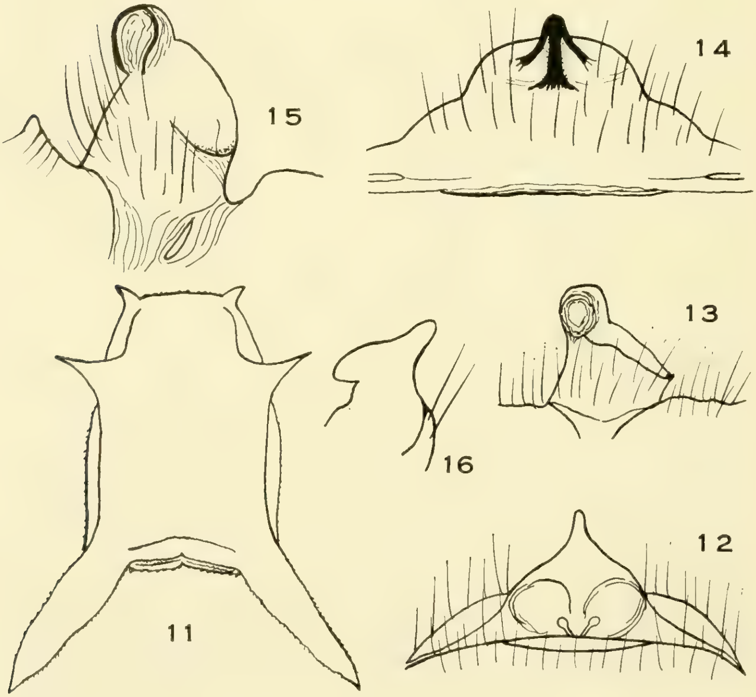


Fig. 11. Dorsal view of abdomen, taken from type of *M. flavomaculata* (Keyserling).

Figs. 12-13. Epigynum of type of *M. flavomaculata* (Keyserling) from behind, and in profile from right side, respectively.

Figs. 14-15. Epigynum of typical *M. forcipata* from Cuba from below, and in profile from right side, respectively.

Fig. 16. Palpal tarsal hook of male, nearly posterior view.

the typically claviform, long, posterior spines may show no distal swelling. The appearance of the epigynum (Figures 12-15) seems to be consistent. Cephalic part of carapace somewhat raised; median fovea a well-defined oval pit transversely situated; three pairs of dorsolateral foveae are developed in varying degrees in different specimens. Sternum with a well-defined, small, posterior tubercle.

Male. There may still be some doubt about the correct matching of the sexes in this species, as concluded by Miss Bryant, but I think it highly probable that she was correct. Her figures 141 and 146 show the male abdomen and palpus. The palpal tarsal hook is shown in Figure 16 in this paper. Contrary to Miss Bryant's statement concerning the absence of a ventral hook on the first coxa, I find a moderately well-developed hook together with the expected chitinized ridge and groove on the prolateral surface of the second femur near the proximal end. The male color pattern appears to be modified from that of the female.

Collection records. Males are rare in collections; I have seen only the specimen described by Miss Bryant. Females have been taken in many localities in Cuba. I have seen a female from Carrefour, Haiti, collected by A. F. and M. H. Archer on July 22, 1955, and another female taken two miles east of Cayes du Jacmel, Haiti, Sept. 2, 1935, by W. G. Hasler.

MICRATHENA GENTILICIA sp. nov.

Figures 17-22

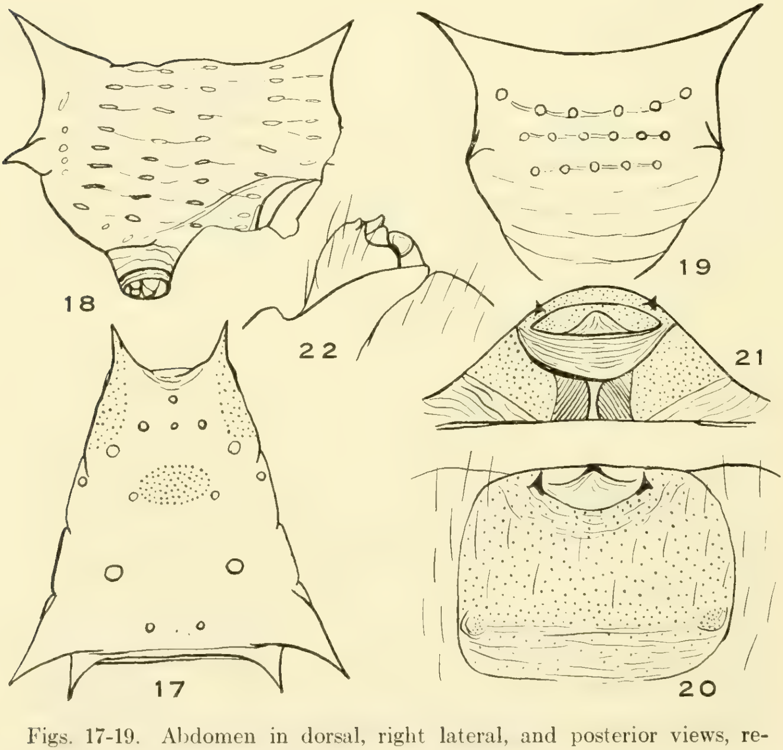
The specific name *gentilicia* is a Latin adjective meaning belonging to the group.

Female holotype. Total length 4.55 mm to posterior end of lower posterior spines; total length to posterior end of abdomen between these spines 4.36 mm. Carapace 1.76 mm long; 1.17 mm wide just behind second coxae where it is widest; about 0.59 mm tall; the median fovea is a small, shallow pit; without dorsolateral foveae.

Eyes. Viewed from above, anterior row strongly recurved, posterior row moderately so; viewed from in front, anterior row nearly straight, posterior row strongly procurved, all measured from center. Median eyes on a moderately raised tubercle; lateral eyes likewise. Central ocular quadrangle wider behind than in front in ratio of 14:9; wider behind than long in ratio of 14:11. Ratio of eyes AME:ALE:PME:PLE = 5:5:9:6 (lateral eyes very oval; long diameters used for measurements). AME separated from one another by about five-thirds of their diameter, from ALE by about four times their diameter. PME separated from one another by a little more than one and one-half times their diameter, from PLE by about nine-fourths of their diameter. Laterals separated from one another by the radius of ALE. Height of clypeus equal to eight-fifths of the diameter of AME.

Chelicerae. Short, fairly robust; quite gibbous in front in basal half; impossible to view teeth on margins of fang groove without damage to holotype; a paratype has four teeth on promargin with

External Anatomy of *Micrathena*
Figures 17-22, *M. gentilicia*



Figs. 17-19. Abdomen in dorsal, right lateral, and posterior views, respectively.

Figs. 20-22. Epigynum from below, in posterior view, and in profile, right side, respectively.

the largest in third place from base of fang, and three teeth on the retromargin with all nearly uniform in size.

Sternum. Quite convex; lateral tubercles not evident; not continued between fourth coxae, which are separated by only about one-sixth of their width.

Legs. 4123. Width of first patella at knee 0.17 mm, tibial index of first leg 12. Width of fourth patella at knee 0.19 mm, tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
		(All measurements	in millimeters)			
I.	1.36	0.53	0.86	0.84	0.53	4.12
II.	1.28	0.51	0.75	0.75	0.53	3.82
III.	0.90	0.35	0.52	0.51	0.44	2.72
IV.	1.65	0.48	0.95	0.99	0.55	4.62

Legs with few spines but with many setigerous tubercles. Numerous trichobothria on tibiae, metatarsi, and tarsi.

Abdomen. General form with spination shown in Figures 17-19. There is no evidence of additional small spines on available paratypes.

Epigynum. Rather complicated; the pattern has not been seen in other species (Figs. 20-22).

Color in alcohol. Carapace brownish, darker through median region; much darker along ventrolateral margins. Sternum yellowish with black flecks and irregular black spots. Legs brownish with variations. Abdomen with a complicated color pattern: there is an oval, central, dorsal, white spot (stippled in Fig. 17); the lateral sides of the anterior spines and adjacent lateral abdominal walls are whitish; additional pairs of white spots on the dorsum and lateral sides are irregular, somewhat indefinite and difficult to describe adequately, and probably highly variable; the venter is nearly black through the broad center, with white on each side.

Type locality. The holotype and three paratype females were collected in Trinidad, W. I., between 1934 and 1936, by N. A. Weber but no further data are given on the labels. The male is not known.

MICRATHENA GERTSCHI sp. nov.

Figures 23-29

Male holotype. Total length about 4.55 mm (body somewhat distorted). Carapace 1.78 mm long; 1.20 mm wide opposite interval between second and third coxae where it is widest; with the usual nearly circular central fovea; somewhat overlapped by anterior border of abdomen; essentially typical of males of the genus.

Eyes. Lateral tubercles moderately well developed; AME located on a well-developed tubercle considerably extended forward over the clypeus. Viewed from above, both rows strongly recurved; viewed from in front, anterior row gently recurved, posterior row gently procurved; all measured from center. Central ocular quadrangle wider behind than in front in ratio of 20:17; nearly as long as wide behind. Ratio of eyes AME:ALE:PME:PLE = 6:5:7:4.5 (laterals irregular in outline). AME separated from one another by about 1.5 times their diameter, from ALE by about ten-thirds of their diameter. PME separated from one another by about nine-sevenths of their diameter, from PLE by about three times their diameter. Laterals separated from one another by about one-third of the diameter of PLE. Clypeus strongly receding; height equal to about twice the diameter of AME.

Chelicerae, Maxillae, and *Lip.* Difficult to examine without injury to the holotype; apparently typical of males of the genus.

Sternum. Oval in general outline; extended between all coxae; fourth coxae separated by two-thirds of their width; with numerous stiff, black bristles.

Legs. 1423. Width of first patella at knee 0.16 mm, tibial index of first leg 11. Width of fourth patella at knee 0.14 mm, tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
	(All measurements in millimeters)					
I.	1.54	0.44	1.06	0.91	0.42	4.37
II.	1.39	0.40	0.81	0.70	0.41	3.71
III.	0.77	0.29	0.35	0.44	0.31	2.16
IV.	1.54	0.35	0.81	0.88	0.42	4.00
Palpus	0.31	0.13	0.15	——	0.55	1.14

The characteristic ventral spines on the first and second tibiae are shown in Figures 24 and 26. Spines on the first femur as seen in prolateral view are shown in Figure 25. The ventral hook on the first coxa is small and pointed; the corresponding prolateral, chitinized ridge and groove on the second femur are moderately well developed near its proximal end. Trichobothria occur on the tibiae but not elsewhere.

Palpus. Figures 27-29. The basal tarsal hook appears to be distinctive. The tibia is conservative.

Abdomen. Figure 23; only slightly flattened dorsoventrally; the spinnerets are located only a little behind the middle of the venter and are surrounded by a poorly chitinized ring.

External Anatomy of *Micrathena*
Figures 23-29, *M. gertschi*

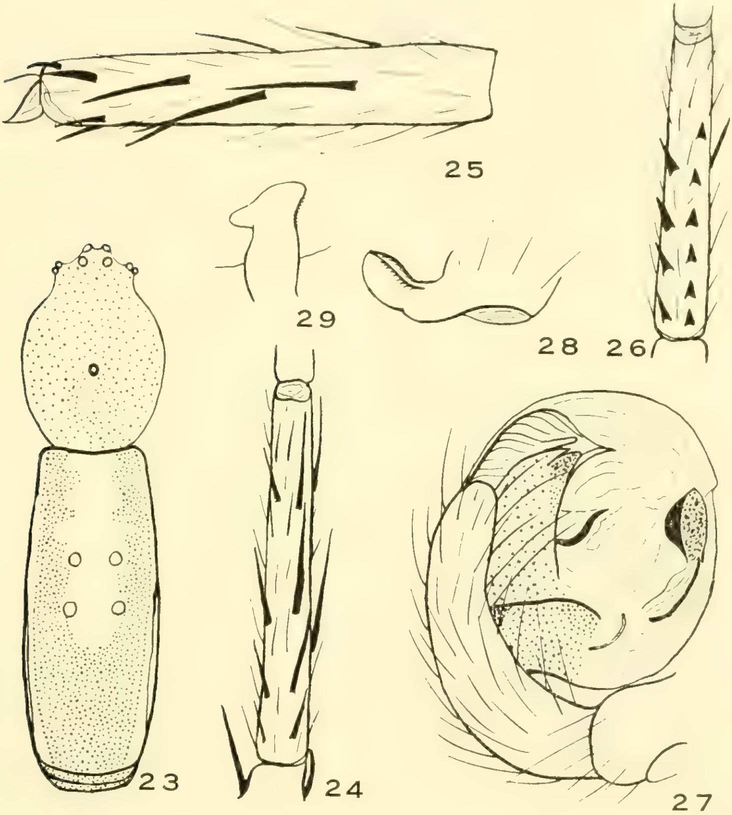


Fig. 23. Body of male, dorsal view.
Fig. 24. Right first tibia, ventral view.
Fig. 25. Right first femur, prolateral view.
Fig. 26. Right second tibia, nearly ventral view.
Fig. 27. Left palpal tarsus.
Fig. 28. Left basal palpal tarsal hook and base of cymbium.
Fig. 29. The same from nearly posterior view.

Color in alcohol. Legs yellowish with variations. Mouth parts brownish. Palpi like legs except that cymbium is very dark brown. Carapace medium brown with fine, dark, irregular dots; a lighter area extends from the median fovea to the posterior border. The sternum is brown with darker streaks. Abdomen: the dorsum is brown with a nearly white spot in the middle and a light streak extending through the middle from the white spot to the anterior border; the sides are yellowish with many irregular, whitish flecks; the venter has a brownish median stripe with many small, yellowish flecks.

Type locality. The holotype male is from Simla, Trinidad, W. I., December 12, 1954 (A. M. Nadler).

Other records. One paratype male is also from Simla, February 26, 1959 (A. M. Nadler), and another is from Diego-Martin, Trinidad, W. I., Sept. 8, 1946 (R. H. Montgomery). The female is unknown.

MICRATHENA LEPIDA sp. nov.

Figures 30-34

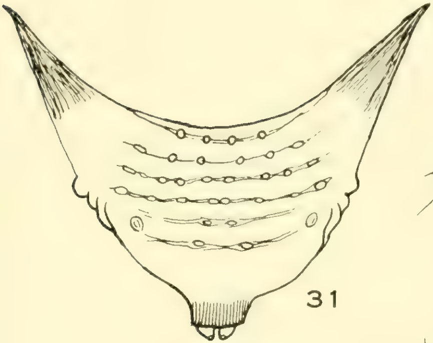
Several females of a single species have recently been found in a collection in the Museum of Compartive Zoology, all taken on the Island of Trinidad, W. I., by R. Thaxter and Dr. P. J. Darlington, Jr. The males described in this paper as *M. nitida* were found with some of these females and there is a suspicion that they belong together. However, as several other kinds of females were also present in the collection, it seems undesirable to unite *M. lepida* and *nitida* until there are more data regarding their relationship. One of the females has been selected as the holotype of *M. lepida.* This species appears to belong in the group including *M. sagittata* (Walckenaer) and *M. gladiola* (Walckenaer). The name *lepida* is a Latin adjective meaning pleasant.

Female holotype. Total length to posterior border of abdomen 5.56 mm; to tips of posterior spines 6.05 mm. Carapace considerably overlapped by anterior end of abdomen; about 2.28 mm long; about 1.95 mm wide opposite second coxae where it is widest; median fovea hardly visible as a shallow depression; without dorsolateral foveae; of moderate height; without gibbosity posterior to median fovea; ocular tubercles only moderately developed.

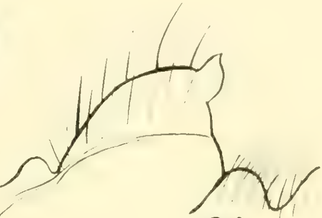
Eyes. Posterior row slightly longer than anterior row. Viewed from above, anterior row strongly recurved, posterior row only moderately so. Viewed from in front, anterior row nearly straight, posterior row moderately procurved, all measured from center. Ratio of eyes AME:ALE:PME:PLE = 10:8.5:12:8.5. AME separated from one another by their diameter, from ALE by nearly four times their diameter. PME separated from one another by slightly more than 1.5 times their diameter, from PLE by nearly

External Anatomy of *Micrathena*

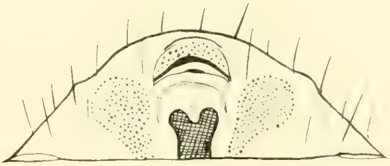
Figures 30-34, *M. lepida*



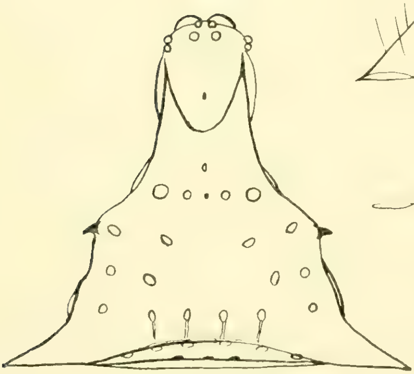
31



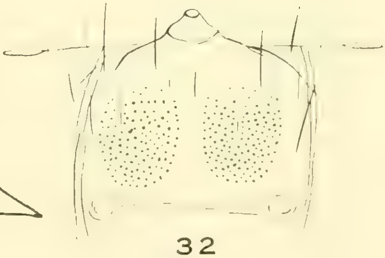
34



33



30



32

Fig. 30. Body of female, dorsal view.

Fig. 31. Posterior end of abdomen of female.

Figs. 32-34. Epigynum from below, in posterior view, and in profile, right side, respectively.

three times their diameter. LE separated from one another by a little less than their radius. Central ocular quadrangle wider behind than in front in ratio of about 10:7; wider behind than long in ratio of about 4:3. Height of clypeus equal to slightly more than the diameter of AME.

Chelicerae. Moderately robust, parallel, with basal boss well developed as a chitinous ridge; fang groove with four teeth along promargin and three along retromargin.

Lip. Wider than long in ratio of about 11:6, reaching somewhat beyond middle of maxillae.

Sternum. Scutiform as usual; moderately convex but not raised into a cone as in *M. gladiola* (Walckenaer); lateral tubercles only moderately developed; not extended between fourth coxae, which are separated by slightly more than one-half of their width; sternal suture gently procurved.

Legs. 4123. Width of first patella at knee 0.22 mm, tibial index of first leg 11. Width of fourth patella at knee 0.24 mm, tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
		(All measurements in millimeters)				
I.	2.02	0.72	1.30	1.20	0.65	5.89
II.	1.95	0.65	1.11	1.11	0.59	5.41
III.	1.37	0.46	0.73	0.72	0.55	3.83
IV.	2.47	0.65	1.25	1.43	0.72	6.52

Legs with few spines but with many setigerous tubercles; especially true of femora.

Abdomen. Closely resembling that of *M. gladiola* (Walckenaer), but distinct (Fig. 30). There are three pairs of spines, but no indications of the small posterior spines that occur on both *M. sagittata* and *M. gladiola.*

Epigynum. Figures 32-34. Variation of this organ may be caused by injuries incurred in handling.

Color in alcohol. Carapace reddish brown with irregular lighter and darker streaks. Legs light reddish brown, lighter beneath. Abdomen yellowish white dorsally with usual "punctures"; spines reddish; sides with alternating, narrow, black and yellowish-white stripes bordering the longitudinal grooves; posterior surface essentially the same. Color pattern probably variable in a large population.

Type locality. The holotype female is from Port-of-Spain, Trinidad, W. I., April 1913 (R. Thaxter).

Other records. Six paratype females were collected with the holotype from Mt. Tucuche, Trinidad, April 1929 (P. J. Darlington, Jr.). A female in the British Museum (Natural History) thought to belong to this species, was collected by Capt. A. K. Totten of H.M.S Rodney, January 2, 1931, in Maracas Valley, Moran Pool. Trinidad. The male is not known.

MICRATHENA LEVII sp. nov.

Figures 35-40

Male holotype. Total length 3.8 mm. Carapace 1.69 mm long; 1.41 mm wide opposite interval between second and third coxae where it is widest; much narrowed at posterior border; smoothly rounded along margins and dorsum; median fovea hardly discernible; not overlapped by anterior border of abdomen.

Eyes. Lateral ocular tubercles moderately well developed; central ocular tubercle also moderately well developed with AME extended forward to make clypeus very receding. Viewed from above, both rows rather strongly recurved; viewed from in front, anterior row gently recurved, posterior row definitely procurved, all measured from center. Central ocular quadrangle wider behind than in front in ratio of nearly 3:2; wider behind than long in ratio of about 27:22. Ratio of eyes AME:ALE:PME:PLE = 6.5:6:8:5. AME separated from one another by nearly their diameter, from ALE by about three times their diameter, from PLE by nearly 2.5 times their diameter. Laterals separated from one another by about one-third of the diameter of PLE. Height of clypeus equal to about 2.7 times the diameter of AME.

Sternum. Only slightly convex; finely rugulose; with the usual sparse covering of stiff bristles; scutiform in general but continued between all coxae; fourth coxae separated by about two-fifths of their width.

Legs. 4123. Width of first patella at knee 0.15 mm, tibial index of first leg 14. Width of fourth patella at knee 0.12 mm, tibial index of fourth leg 12.

(All measurements in millimeters)

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
I.	1.19	0.40	0.68	0.66	0.44	3.37
II.	1.17	0.37	0.62	0.59	0.40	3.15
III.	0.73	0.29	0.46	0.40	0.33	2.21
IV.	1.32	0.33	0.68	0.73	0.42	3.48
Palpus	0.27	0.13	0.14	——	0.62	1.16

The length of the palpal tarsus as given in the above table includes the extended basal hook. There is no ventral hook on the first coxa and no chitinized, prolateral ridge and groove on the second femur as so often occurs in this genus. The ventral spines on the first and second tibiae are shown in Figures 36-37. Trichobothria on the dorsal surfaces of the tibiae are apparently arranged in two rows.

External Anatomy of *Micrathena*
Figures 35-40, *M. levii*

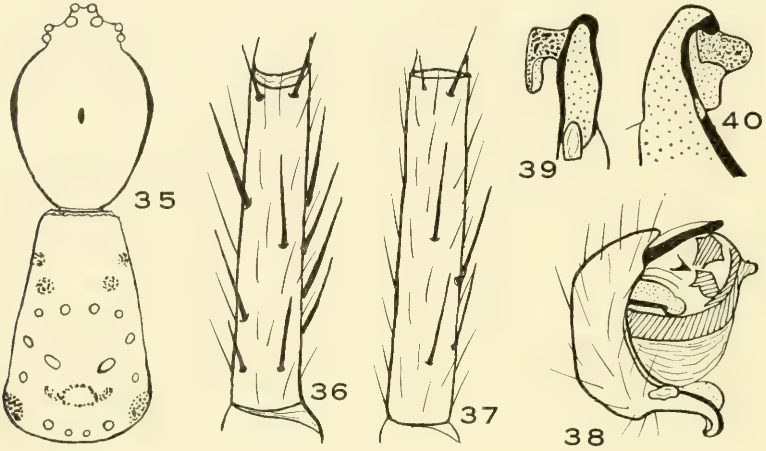


Fig. 35. Body of male, dorsal view.
Fig. 36. Left first tibia, ventral view.
Fig. 37. Left second tibia, ventral view.
Fig. 38. Left palpal tarsus.
Figs. 39-40. Two different views of palpal basal tarsal hook.

Palpus. Figures 38-40. I have not seen this type of basal tarsal hook in any other species. Both tibia and patella are short with the tibia relatively very broad and somewhat trilobed.

Abdomen. Figure 35. Moderately flattened dorsoventrally with no distinct indication of suppressed spines.

Color in alcohol. Legs medium brown with variations. Carapace medium brown with fine, irregular, dark dots. Sternum brownish with irregular, white, deposits. Abdomen dorsum yellowish with irregularly placed, white spots; as indicated in Figure 35 there is a series of irregular grayish spots also on the dorsum; the venter in front of genital groove and the sclerotized ring around the spinnerets are brown, but behind the genital groove the color is yellowish with irregular gray lines and spots.

Type locality. Male holotype is from Simla, Trinidad, W.I., February 26, 1959 (A. M. Nadler). The female is unknown.

MICRATHENA MILITARIS (Fabricius), 1775
Figures 41-50

Aranea militaris Fabricius, 1775. Holotype from America. Probably in the Copenhagen Natural History Museum.

Plectana militaris, Walckenaer, 1841.

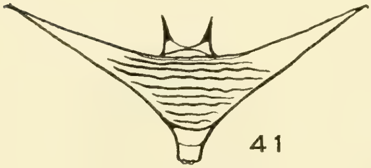
Micrathena militaris. Petrunkevitch, 1911; Reimoser, 1917; Petrunkevitch, 1926, 1930; Bryant, 1940; Roewer, 1942; Bryant, 1945; Bonnet, 1957.

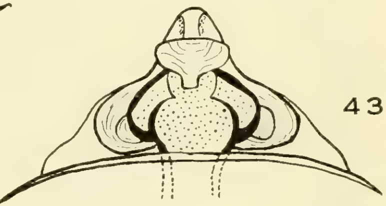
Micrathena armata, Bryant, 1940, 1945 [not *Aranea armata* Olivier].

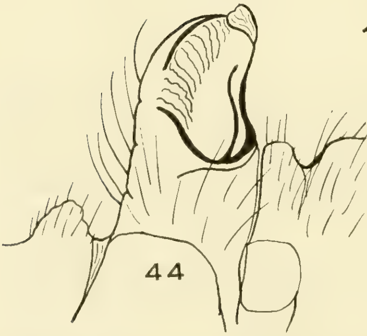
Much confusion has existed concerning the status of what is generally regarded as *M. militaris.* The species has often been filed in collections as *M. sagittata* and *M. forcipata* (Thorell), frequently as *M. militaris.* Miss Bryant regarded *M. armata* (Olivier) as a synonym of *M. militaris,* and her conclusion has generally been followed. Dr. Petrunkevitch (1926) may have had the species from the Virgin Islands but his figure of the epigynum does not agree with the specimens I have studied from Cuba, Haiti, and the Dominican Republic. I am not able to clarify the confusion but I can point out certain inconsistencies. I have noted in the epigyna significant differences between typical females from Cuba and specimens from Haiti and the Dominican Republic. These differences may be observed by a comparison of Figures 42-44 with Figures 45-47. Miss Bryant (1940) described what she regarded as the male of the species; some have doubted the validity of her identification, but, after examination of several males from Haiti, the Dominican Republic, and Puerto Rico, taken with females from these same regions, I am ready to accept her conclusion until we have definite evidence to the contrary. I have been unable to find males from Cuba that can be definitely associated with females from that island, and this again emphasizes the need for intensive field work in the whole West Indian region.

Females. Total length of a specimen from Cuba is 7.61 mm from AME to posterior border of abdomen between the large posterior spines; total length from anterior border of somewhat gibbous bases of chelicerae to the tips of the posterior spines 11.83 mm. Considerable variation in size of mature females has been noted. The two pairs of spines shown in Figure 41 and in Petrunkevitch's figure (1926) are those to which reference is usually made. Frequently, however, a pair of very small dorsolateral spines occurs about half way between the bases of the long, posterior spines and the much smaller, very erect anterodorsal spines. Less frequently another very small spine occurs at about the base of each of the large posterior spines and is directed posteriorly. The promargin of the fang groove on a fairly typical female from Haiti bears five teeth, three of which are relatively small and placed somewhat irregularly; the retromargin bears three teeth of moderate size, regularly placed. The Cuban specimen chosen to show the features of the epigynum has four teeth on the promargin and three on the retromargin. Females frequently have an embolus and accompanying sheath caught in one receptacle, and, occasionally, an embolus in each receptacle, an occurrence first reported for this species by Petrunkevitch in his study of the species in Puerto Rico. The sternum is rugulose; it has three pairs of prominent tubercles and terminates in a prominent, median, extended, conical tubercle. The most puzzling variations of all concern the epigynum: Figures 42-44 show its appearance in a female selected from many specimens collected in the Dominican Republic, viewed in three different positions; Figures 45-47 show its appearance in a female collected in Havana, Cuba. My brief study of numerous specimens from several islands in the West Indies certainly suggests the possibility that what is now regarded as one species may, upon further study, be divided into two or more.

External Anatomy of *Micrathena*
Figures 41-44, *M. militaris*







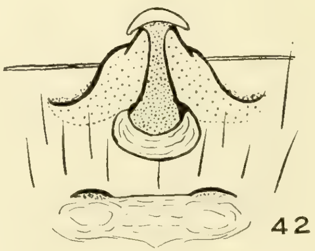
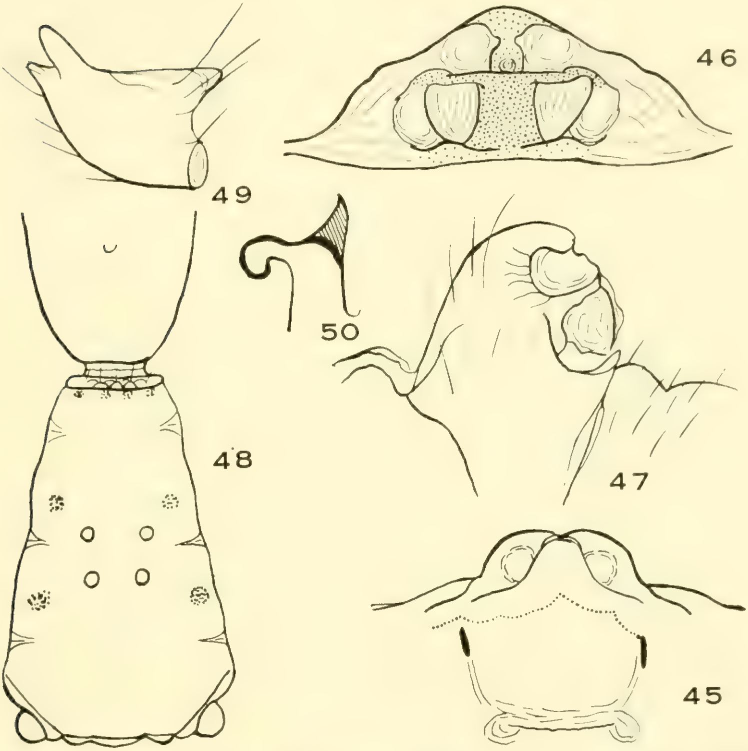


Fig. 41. Abdomen viewed from posterior end.

Figs. 42-44. Epigynum from below, in posterior view, and in profile from right side, respectively (Fig. 44 more enlarged).

External Anatomy of *Micrathena*
Figures 45-50, *M. militaris*



Figs. 45-47. Epigynum from below, in posterior view, and in profile from right side, respectively (specimen from Cuba).

Fig. 48. Dorsal view of abdomen of male.

Fig. 49. Left palpal tibia.

Fig. 50. Left palpal basal tarsal hook.

Male. Total length 3.95 mm. The sternum is irregularly rugulose; the tubercles, so prominent in the female, are present but much less developed. The teeth along the fang groove differ from those of the female; the promargin appears to bear four teeth; the retromargin has four teeth with the distal two set very close together. Figure 48 shows the form of the abdomen as viewed from above. Figures 49-50 show the important features of the palpal tibia and basal tarsal hook. There is no ventral hook on the first coxa and no corresponding chitinized ridge and groove on the second femur.

Collection records. The male described here and the female from which Figures 42-44 were taken, were collected at Jarabacoa, La Vega, Dominican Republic, May 11, 1959, by Drs. M. W. Sanderson and T. H. Farr. The female from which Figures 45-47 were taken was collected in Havana, Cuba, with no date indicated, and was originally identified as *M. armata* (Olivier). Numerous specimens have been studied from Cuba, Puerto Rico, Haiti, and the Dominican Republic.

MICRATHENA NITIDA sp. nov.

Figures 51-56

The males described below were, for a time, regarded as *M. macilenta* Chickering, described from Panama, but after a more careful study and direct comparison it now seems quite certain that we are dealing with a new, closely related species.

The name *nitida* is a Latin adjective meaning elegant.

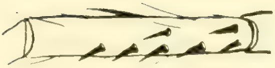
Male holotype. Total length 4.03 mm. Carapace 1.6 mm long, 1.3 mm wide opposite interval between second and third coxae where it is widest; with eyes on moderately well-developed tubercles; the moderately well-developed median fovea is nearly a round pit; with no dorsolateral foveae; nearly flat along the middle from PME to posterior declivity; very finely granulated.

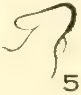
Eyes. Posterior row only slightly wider than anterior row. Viewed from above, both rows strongly recurved. Viewed from in front, anterior row nearly straight, posterior row moderately procurved, all measured from center. Ratio of eyes AME:ALE:PME:PLE = 5.5:5:7.5:5. AME separated from one another by slightly more than their diameter, from ALE by slightly less than three times their diameter. PME separated from one another by five-sevenths of their diameter, from PLE by about twice their diameter. LE separated from one another only by a broad line. Central ocular quadrangle wider behind than in front in ratio of about 6:5; about as long as wide behind. Clypeus very receding; height of clypeus equal to about twice the diameter of AME.

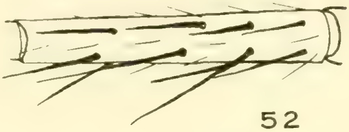
Sternum. Generally oval in outline with the usual scalloped margin; extended between fourth coxae, which are separated by about three-fourths of their width.

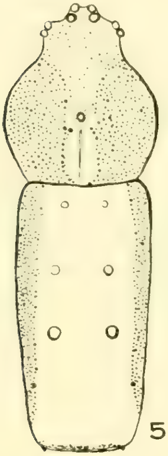
Legs. 1423. Width of first patella at knee 0.13 mm, tibial index of first leg 11. Width of fourth patella at knee 0.11 mm, tibial index of fourth leg 11.

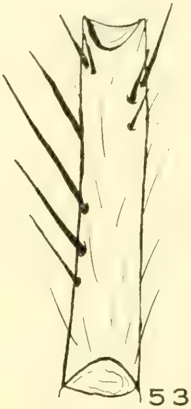
External Anatomy of *Micrathena*
Figures 51-56, *M. nitida*


54


56


52


51


53

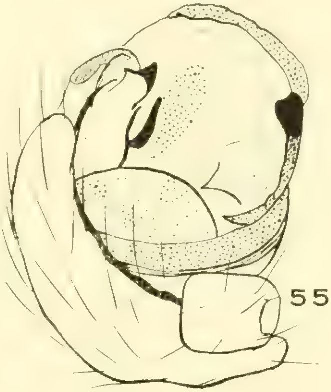

55

Fig. 51. Body of male, dorsal view.
Figs. 52, 54. Left first and second tibia, respectively, ventral view.
Fig. 53. Left first femur, ventral view.
Fig. 55. Left palpal tibia and tarsus.
Fig. 56. Palpal basal tarsal hook, nearly posterior view.

(All measurements in millimeters)

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
I.	1.25	0.39	0.81	0.70	0.40	3.55
II.	1.10	0.37	0.60	0.55	0.35	2.97
III.	0.73	0.29	0.37	0.37	0.29	2.05
IV.	1.32	0.33	0.65	0.70	0.39	3.39
Palpus	0.26	0.12	0.14	——	0.48	1.00

First leg with many long robust spines on femur and tibia (Figs. 52-53); second leg with short robust spines on tibia (Fig. 54); first coxa with a ventral hook and second femur with the corresponding prolateral ridge and groove, all moderately well developed; fourth leg with long spines on femur, patella, and tibia, but less developed than on first and second legs; a few other spines also present. Two trichobothria observed on the dorsal side of all tibiae.

Palpus. Details rather closely resemble those of palpi of several other species, but there are specific differences somewhat difficult to represent adequately in drawings (Figs. 55-56).

Abdomen. Much flattened in the manner common among males in this genus; with general form as shown in Figure 51; with obscure indications of suppressed spines at posterior end.

Color in alcohol. Legs and mouth parts with varying shades of light brown and yellowish brown. Carapace medium brown with black flecks except for a light stripe extending posteriorly from the median fovea. Abdomen: dorsum yellowish with a narrow dark marginal stripe on each side; venter yellowish with a narrow dark lateral stripe.

Type locality. The holotype male is from Trinidad, W.I., near Port-of-Spain, April, 1913 (R. Thaxter). Several paratype males are in the collection from Trinidad; one is from Sangre Grande, April, 1913 (R. Thaxter); another is from Port-of-Spain, February, 1926 (W. S. Brooks); the remainder are from the same locality as the holotype and, apparently, taken at about the same time.

MICRATHENA PRAETERITA sp. nov.

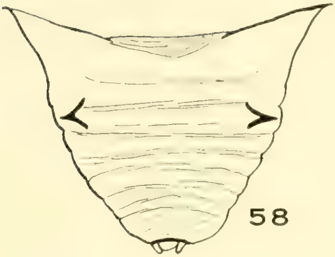
Figures 57-63

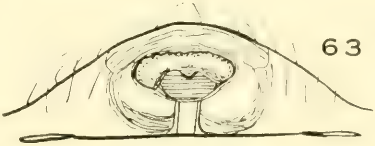
The holotype described here together with numerous paratypes came to me identified as *M. bicolor* (Keyserling). There are superficial resemblances, but the details of structure indicate clearly that these specimens do not belong with Keyserling's species. During my period of work in the British Museum (Natural History) in 1958 I was able to study Keyserling's types of *M. bicolor*. This acquaintance has helped me to determine that the species has never been described. The specific name *praeterita* is a Latin adjective meaning not noticed.

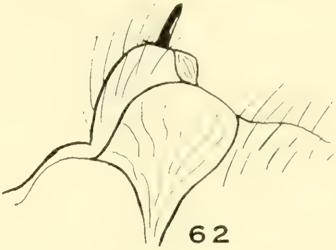
Female holotype. Total length, including the slightly extended bases of the chelicerae 4.75 mm. Carapace 1.7 mm long; 1.01 mm wide opposite posterior border of second coxae where it is widest; with indistinct median fovea a short, shallow groove; with no special features; without dorsolateral foveae; cephalothoracic groove very indistinct.

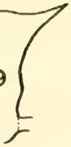
Chelicerae. Moderately well developed; without special modifications; typical of females of the genus; fang groove well defined; in a paratype the promargin of the fang groove has three teeth, the middle one of which is considerably the largest; the retromargin also has three teeth in this paratype, with the one nearest the base of the fang somewhat the largest.

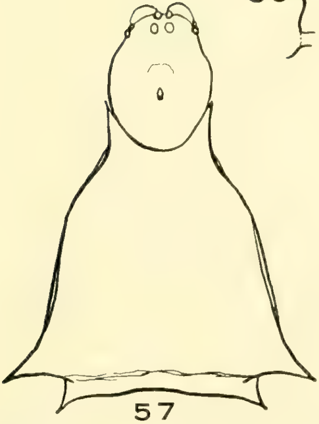
External Anatomy of *Micrathena*
Figures 57-63, *M. praeterita*

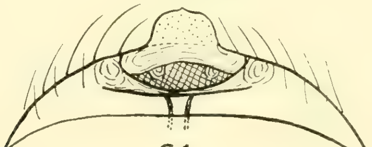

58


63


62


59


57


61

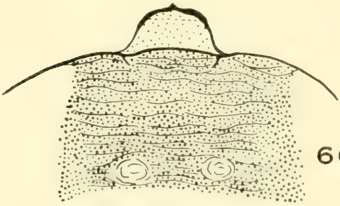

60

Fig. 57. Body of female, dorsal view.
Fig. 58. Posterior end of abdomen.
Fig. 59. Lateral view of right anterior abdominal spine.
Figs. 60-62. Epigynum of holotype from below, in posterior view, and in profile from right side, respectively.
Fig. 63. Appearance of epigynum after loss of thin, projecting shelf.

Maxillae. Short, broad, parallel; also typical of females of the genus.

Lip. Wider than long in ratio of about 9:5; does not quite reach to middle of maxillae.

Sternum. Scutiform in general; sternal suture strongly procurved; moderately convex; not continued between coxae; terminates in a point at beginning of space between fourth coxae, which are separated by nearly one-fourth of their width.

Legs. 4123. Width of first patella at knee 0.21 mm, tibial index of first leg 15. Width of fourth patella at knee 0.21 mm, tibial index of fourth leg 14.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
		(All measurements in millimeters)				
I.	1.38	0.53	0.86	0.81	0.54	4.12
II.	1.28	0.48	0.77	0.75	0.53	3.81
III.	0.92	0.35	0.53	0.44	0.35	2.59
IV.	1.65	0.51	0.95	0.99	0.62	4.72

The palpal claw is finely pectinated. Spines are nearly absent from the legs; setigerous tubercles are moderately well developed. Trichobothria have been clearly observed only on the tibiae.

Abdomen. Figures 57-59. The three pairs of spines resemble those of some other species, but there are also distinctive features among these. Additional spines, frequently found in certain other species, are either rare or lacking altogether in this species.

Epigynum. Figures 60-62 illustrate the holotype. Note that the thin shelf extending ventrally from beneath the ventral border is frequently lacking in paratype, presumably because of breakage. In paratypes that have lost this part the superficial appearance of the organ is quite different. Figure 63 is intended to show the appearance of the epigynum in posterior view on an individual that has lost the shelf and probably was also under greater internal pressure than was the holotype.

Color in alcohol. The legs are medium brown with variations. Mouth parts are much the same. The carapace is brown with radiating darker streaks and a darker median stripe leading from PME nearly to the median fovea. All of these marks are poorly defined. The sternum is brownish with dark streaks and spots throughout. Abdomen with a white, black and brown color pattern difficult to describe adequately; the dorsum has an elongated white spot along the posterolateral side of each of the anterior spines; a narrow, irregular, brown stripe extends along the median side and dorsal surface of each of the anterior spines and reaches back nearly to the middle of the dorsum; an irregular white stripe extends between the two anterior spines and along the middorsal surface to nearly opposite the bases of the large posterior spines; lateral to these marks there is a mixture of white and brown patches; between the bases of the large posterior spines there is a transverse row of five white patches; the venter has a broad, black stripe extending from the genital groove and dividing to extend dorsally for a considerable distance as a pair of black stripes directed toward the small posterior spines. Considerable variation in the color pattern has been noted among the paratypes as would be expected. For example, the irregular white stripe in the dorsum of the holotype may be broken into white spots by encroachment of the brown color that laterally bounds the white: the brown color may be reduced with an increase in the white until the latter predominates.

Type locality. The female holotype is from St. Augustine, Trinidad, W.I., September 18, 1946 (R. H. Montgomery). Nineteen paratype females were, apparently, collected with the holotype. The male is unknown.

MICRATHENA RUFOPUNCTATA (Butler), 1873
Figures 64-67

Acrosoma rufopunctatum Butler, 1873. Holotype from Jamaica, sex not indicated, in British Museum (Nat. Hist.).

Micrathena rufopunctata Petrunkevitch, 1911; Reimoser, 1917; Roewer, 1942; Bonnet, 1957.

The author of this species gave a very inadequate description unaccompanied by figures. Reimoser (1917) merely repeated the original description. There has never been any detailed description published.

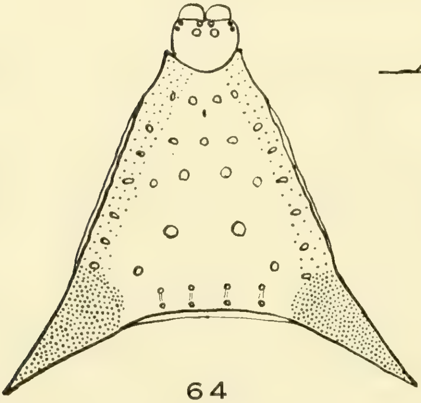
Female. Total length 5.85 mm, including the bases of the somewhat convex chelicerae and relatively long posterior abdominal spines. Carapace: largely overlapped by extended dorsal portion of abdomen and anterior spines; median thoracic fovea a small, rounded pit; with a series of faintly indicated dorsolateral foveae.

Eyes. Viewed from above, anterior row moderately recurved, posterior row slightly so. Viewed from in front, anterior row slightly recurved, posterior row moderately procurved, all measured from center. Central ocular quadrangle wider behind than in front in ratio of 25 : 21; wider behind than long in ratio of 25 : 23. Ratio of eyes AME : ALE : PME : PLE = 7.5 : 6.5 : 8.5 : 6. AME separated from one another by slightly less than their diameter, from ALE by about four times their diameter. PME separated from one another by nearly seven-sixths of their diameter, from PLE by slightly more than three times their diameter. Laterals separated from one another by about one-third of the diameter of PLE. Height of clypeus about equal to the diameter of AME.

Sternum. A simple scutiform; sternal suture slightly procurved; with anterolateral tubercles moderately developed; with a minute tubercle opposite each coxae 1-3 and another minute tubercle at blunt posterior end, which is not extended between fourth coxae; fourth coxae separated by about one-third of their width.

Legs. 4123. Width of first patella at knee 0.25 mm, tibial index of first leg 15. Width of fourth patella at knee 0.21 mm, tibial index of fourth leg 14.

External Anatomy of *Micrathena*
Figures 64-67, *M. rufopunctata*



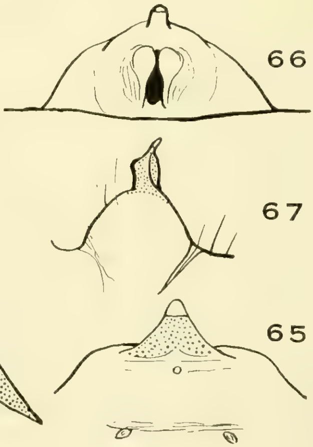


Fig. 64. Body of female, dorsal view.

Figs. 65-67. Epigynum from below, in posterior view, and in profile from right side, respectively.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
		(All measurements in millimeters)				
I.	1.54	0.62	1.01	1.08	0.53	4.78
II.	1.45	0.57	0.88	0.95	0.53	4.38
III.	0.97	0.40	0.53	0.55	0.44	2.89
IV.	1.76	0.55	0.92	1.10	0.48	4.81

Legs with numerous short, slender spines and many setigerous tubercles. Trichobothria observed on tibiae; doubtful elsewhere. Palpal claw finely toothed.

Abdomen. General form as viewed from above shown in Figure 64. There are only two pairs of spines and no indication of small accessory spines such as often appear in the genus. The anterior border and spines are extended far over the carapace.

Epigynum. In essential features, shown in Figures 65-67, epigynum closely resembles that of *M. mitrata* (Hentz), *M. cubana* (Banks), *M. macfarlanei* Chickering, *M. fidelis* (Banks) and probably others.

Color in alcohol. The color pattern on the abdomen is distinctive. The carapace, mouth parts, and legs are all rich reddish brown with variations. The sternum is dark brown. Abdomen: The dorsolateral sides are bright yellow; this marginal stripe includes the anterolateral spines but stops at the bases of the posterolateral spines; there is also a yellow marginal stripe extending along the posterior border between the two posterolateral spines; the latter spines themselves are rich reddish brown; the remaining dorsal region is grayish, darker around the border, and almost white in the center; the lateral and ventral areas are predominantly very dark brown, almost black; the venter has three pairs of bright yellow spots introduced into the brown background; the most anterior pair of these yellow spots is at the level of the epigynum; the second pair at about the level of the spinnerets; the third pair is near the posterior border. I have seen no color pattern like this among the many species in the genus studied during the past several years.

Collection records. The original specimens were reported from Jamaica, W.I., in 1873. So far as I have been able to determine, the species has not been reported from that time until the present. Three females in the American Museum of Natural History were taken by Dr. T. H. Farr, Institute of Jamaica, Kingston, Jamaica, W.I., at the entrance to Mt. Diablo Forest Reserve, June 29, 1960. The male remains unknown.

MICRATHENA SIMILIS Bryant, 1945

Figures 68-71

Micrathena similis Bryant, 1945. Female holotype from Dominican Republic, Puerta Plata, 30 August, 1938, in the Museum of Comparative Zoology.

This species has been under close scrutiny for some time and its validity as a distinct species is still uncertain. Miss Bryant considered it closely related to *M. cubana* (Banks). It should be restudied when a large series is available. Three specimens are known to me: the holotype, a paratype female from the Dominican Republic, Mt. Diego de Ocampo, North Range, 3000-4000 ft. el., July, 1938 (P. J. Darlington, Jr.); one female from Dominican Republic, Valle de Polo, Prov. de Barahona, August 18, 1935 (W. G. Hasler). The male remains unknown. The epigynum appears quite different than represented by Miss Bryant's figures 8 and 43 (1945).

External Anatomy of *Micrathena*
Figures 68-71, *M. similis*

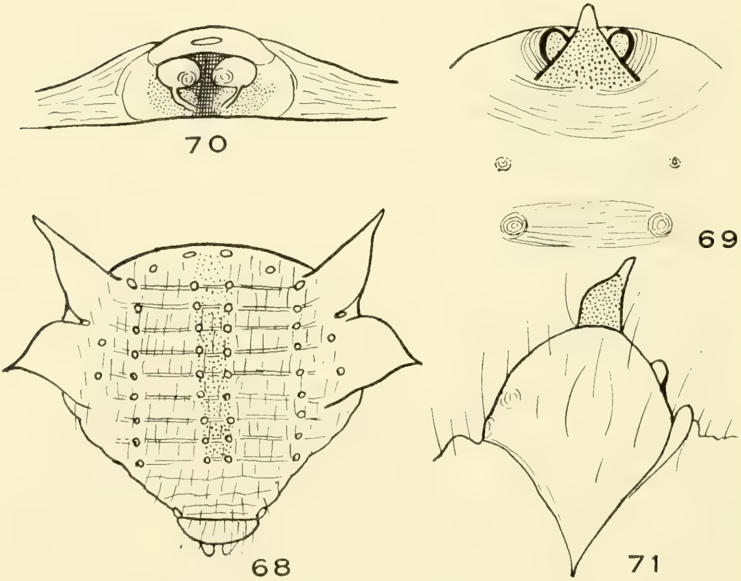


Fig. 68. Posterior end of abdomen from behind.
Figs. 69-71. Epigynum from below, in posterior view, and in profile from right side, respectively.

BIBLIOGRAPHY

BANKS, N.
1909. Arachnida of Cuba. Sec. Rept. Centr. Exper. Stat. Cuba, pp. 150–174, 45 pls.

BONNET, P.
1957. Bibliographia Araneorum. Toulouse. Vol. 2 (3).

BRYANT, ELIZABETH

1940. Cuban spiders in the Museum of Comparative Zoology. Bull. Mus. Comp. Zool., **86**(7): 249–532, 22 pls.

1945. The Argiopidae of Hispaniola. Bull. Mus. Comp. Zool., **95**(4): 359–418, 4 pls.

BUTLER, A. G.

1873. A list of spiders of the genus *Acrosoma*, with descriptions of new species. Proc. Zool. Soc. London, pp. 420–429.

CHICKERING, A. M.

1960a. Three new species of *Micrathena* (Araneae, Argiopidae) from South America. Breviora, Mus. Comp. Zool., No. **121**: 1–11.

1960b. Notes on certain species of *Micrathena* (Araneae, Argiopidae) from South America. Breviora, Mus. Comp. Zool., No. **122**: 1–7.

1960c. Six new species of *Micrathena* (Araneae, Argiopidae) from South America with notes on known species. Proc. Zool. Soc. London, pp. 65–89, 90 figs.

1961. The genus *Micrathena* (Araneae, Argiopidae) in Central America. Bull. Mus. Comp. Zool., **125**(13): 389–470.

FABRICIUS, J. C.

1775. Systema Entomologiae. Vol. II, pp. 434.

KEYSERLING, GRAF E. VON

1864. Beschreibung neuer und wenig bekannter Arten aus der Familie Orbitelae. Sitzber. naturwiss. Gesell. Isis, Dresden, 1863: 63–98, 119–154, pls. 1–7.

1892. Die spinnen Amerikas. 4. Epeiridae. Nürnberg. Baur & Raspe.

PETRUNKEVITCH, A.

1911. A synonymic index-catalogue of spiders of North, Central, and South America. Bull. Amer. Mus. Nat. Hist., **29**: 1–809.

1926. Spiders from the Virgin Islands. Trans. Connecticut Acad. Arts Sci., **28**: 21–78, 28 figs.

1930. The spiders of Porto Rico. Pt. 2. Trans. Connecticut Acad. Arts Sci., **30**: 159–355, 240 figs.

REIMOSER, E.

1917. Die Spinnengattung *Micrathena* Sundevall. Verh. zool. bot. Gesell. Wien, **67**(¾): 73–160.

ROEWER, C. FR.

1942. Katalog der Araneae. Vol. **1**: 1–1040.

SIMON, E.

1892- Histoire naturelle des Araignées. Deuxième Edition. 2 Vols.
1903. Librarie Encyclopedique de Roret, Paris.

SUNDEVALL, J. C.

1833. Conspectus Arachnidum, p. 14

THORELL, T. T.

1859. Nya exotiska Epeirider. Ofvers K. Vet.-Akad. Förh., pp. 299–304.

WALCKENAER, C. A., BARON DE

1837- Histoire naturelle des insectes aptères. 4 Vols. Paris.
1847.

(Received March 19, 1963.)

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 9

REVISED GENERIC DIAGNOSES OF THE FOSSIL FISHES MEGALICHTHYS AND ECTOSTEORHACHIS (FAMILY OSTEOLEPIDAE).

By Keith Stewart Thomson

With One Plate

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
July 7, 1964

PUBLICATIONS ISSUED BY OR IN CONNECTION WITH THE

MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

BULLETIN (octavo) 1863 — The current volume is Vol. 131.

BREVIORA (octavo) 1952 — No. 204 is current.

MEMOIRS (quarto) 1864–1938 — Publication terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 41 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 28 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained from the Publications Office of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Peters' Check-List of Birds of the World. Volumes 1, 4 and 6 are out of print; volumes 2, 3, 5, 7, 9, 10 and 15 are currently available.

Phylogeny and Evolution of Crustacea. Proceedings of a conference held at Cambridge, Mass., March 6-8, 1962. H. B. Whittington and W. D. I. Rolfe, editors. Cambridge, Mass., 192 pp., 80 figs., 1963. Cloth bound, $6.75.

Fishes of the Gulf of Maine, by Henry B. Bigelow and William C. Schroeder. Washington, viii - 577 pp., 1953. Photo-offset reprint, $6.50.

PUBLICATIONS OF THE BOSTON SOCIETY OF NATURAL HISTORY

The remaining stock of the scientific periodicals of the Boston Society of Natural History has been transferred to the Museum of Comparative Zoology for distribution. Prices for individual numbers may be had upon request.

Bulletin of the Museum of Comparative Zoology

HARVARD UNIVERSITY

Vol. 131, No. 9

REVISED GENERIC DIAGNOSES OF THE FOSSIL FISHES MEGALICHTHYS AND ECTOSTEORHACHIS (FAMILY OSTEOLEPIDAE).

By Keith Stewart Thomson

With One Plate

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
July, 1964

Bull. Mus. Comp. Zool., Harvard Univ., 131 (9) :283-311, July, 1964

No. 9 — *Revised generic diagnoses of the fossil fishes* Megalichthys *and* Ectosteorhachis (*family Osteolepidae*).

By Keith Stewart Thomson[1]

In the course of studies on the morphology of the Rhipidistia (fossil fishes of the order Crossopterygii) I have found it necessary to enquire into the systematics of certain of the forms concerned, notably *Ectosteorhachis* and *Megalichthys* (members of the family Osteolepidae).

The name *Ectosteorhachis* was coined by Cope (1880) for material of a rhipidistian collected in the Permian "red-beds" of Texas. Cope described the type species, *Ectosteorhachis nitidus*, and later (1883) a second species, *E. ciceroneus*, which he differentiated from *E. nitidus* by the nature of the surface ornamentation of the dermal bones of the skull. Hussakof (1911) showed that the two forms actually belong to the same species. Until recently remains of *Ectosteorhachis* were rare, but now a considerable amount of material, particularly in the collections of the Museum of Comparative Zoology, is available for study. *Ectosteorhachis* has only been found in the Lower Permian of the United States, and the principal collections have been made in the Wichita Group (Moran to Belle Plains formations); a single jaw in the Museum of Comparative Zoology was recently collected in the Dunkard Group, Lower Permian, of Clarke Hill, Ohio.

In 1891 Cope decided that his genus *Ectosteorhachis* was indistinguishable from the form known as "*Megalichthys*" — a common Carboniferous genus well known in the European Coal Measures. In more recent times re-study of *Ectosteorhachis*, as Romer (1941) has noted, has led to the suggestion that this form is, after all, a distinct genus. The aim of this paper is to explore this view, by a comparative anatomical study of the two forms; as will be seen, the conclusion reached is that *Ectosteorhachis* should be re-established as a valid genus.

"*Megalichthys*" is a rhipidistian occurring very commonly in the Carboniferous deposits of Europe, where it is frequently found in the ironstone shales associated with workable coal seams, and less commonly in the Carboniferous of North America. Unfortunately, there is considerable confusion concerning the nomenclature of this genus and at the end of this paper I have included a discussion of this problem. The name *Megalichthys* throughout this study is used in the sense of Smith-Woodward (1891) as is, in fact, the common usage of the name.

---

[1] Present address: Department of Zoology, University College, London.

Several species of *Megalichthys* have been described; the discussion of the genus given below is based mainly on the structure of the type species *Megalichthys hibberti* Agassiz. *Megalichthys coccolepis* Young, *intermedius* Woodward, *laticeps* Traquair, and *macropoma* Cope, have been distinguished from *M. hibberti* principally on the relative proportions of the maxillae and gular plates and such distinctions do not affect our present discussion in any way.

During this study, which formed part of my dissertation for the degree of Doctor of Philosophy at Harvard University, I have been greatly assisted by Professor A. S. Romer. I am also grateful to him for the use of the collections and facilities of the Museum of Comparative Zoology. I am indebted to Professor G. G. Simpson for his criticism of the final section of this paper. I must also thank Dr. E. I. White, Keeper of Palaeontology at the British Museum (Natural History), London, who allowed me to spend several weeks studying in his department during the summer of 1962. Mr. H. A. Toombs of the British Museum (Natural History) and Dr. C. D. Waterston of the Royal Scottish Museum, Edinburgh, have also given me assistance and advice; I am particularly grateful to the latter for his efforts to identify for me various specimens from the Hibbert Collection in the Royal Scottish Museum.

Dr. B. Schaeffer of the American Museum of Natural History, Dr. D. Baird of Princeton University, and Dr. P. P. Vaughn of the University of California at Los Angeles have each loaned me specimens from the collections of their various institutions.

I was the recipient of North Atlantic Treaty Organization Science Studentship 3/60/955 from 1960 to 1963 and the Jeffries Wyman Scholarship at Harvard University during 1960/1961 while I was engaged in this study.

MATERIALS

The material of *Ectosteorhachis* used in this study comes largely from the collections of the Museum of Comparative Zoology and was collected in the "red-beds" of North Central Texas (Wichita Group, Lower Permian). Specimens, including the holotype (American Museum of Natural History [AMNH]

7239), were loaned to me by various institutions as acknowledged above.

Of the genus *Megalichthys*, several specimens in the Museum of Comparative Zoology (MCZ), including material of the North American species *M. macropoma*, were used in this study. However, the majority of the material studied is in the collections of the British Museum (Natural History) (BMNH); this includes the specimen (P. 42516) described by Agassiz (1843) in his definition of the genus (see later for discussion of nomenclature).

ECTOSTEORHACHIS

Dermal skull roof.[1] As is the case in other Rhipidistia, the outer enamel and dentine layers of the dermal bones of the skull of *Ectosteorhachis*, especially in the ethmoid region, tend often to be fused into a single covering in such a way as to obliterate any external indication of the sutures between separate bones (cf. Westoll, 1936). However, in the collections of the Museum of Comparative Zoology, there are many specimens (especially MCZ 6498, 6499, 8652, 8661 and 8668) from which this outer layer has been lost due to the process of weathering of the fossils. It has thus been possible to give a more complete description of the pattern of the dermal bones of the skull of this genus than may be given for many genera of Osteolepidae.

The only published figures of the skull of *Ectosteorhachis* are those of Hussakof (1911), and of Cope and Matthew (1915), but these show few details of the dermal bone pattern.

The premaxillary element in *Ectosteorhachis* corresponds to the bone which in certain other Rhipidistia Jarvik (1942, 1944) has termed a "compound" bone, comprising a true premaxilla, a rostral element which encloses the ethmoid commissure of the lateral line system, and probably also the first of the series of nasal bones. This element has been given the unwieldy name of "naso-rostro-premaxilla." Jarvik (1942, p. 347) believes that the interpretation of such a unit as a "dentigerous rostral" (cf. Westoll, 1936, 1937) is probably incorrect.

The supraorbital lateral line, anterior to the parietal bone ("frontal" of Jarvik), is borne upon a series of four separate nasal elements (Fig. 1) which probably represent a reduction from a row of six or seven nasals (cf. *Osteolepis;* Jarvik, 1948) of which the first has been incorporated into the premaxillary unit.

---

[1] Throughout this paper the terminology used for the various dermal elements in the skull will follow the system of Jarvik (1942, 1944) with the exception of the parietal and postparietal bones which are termed by Jarvik "frontal" and "parietal," respectively.

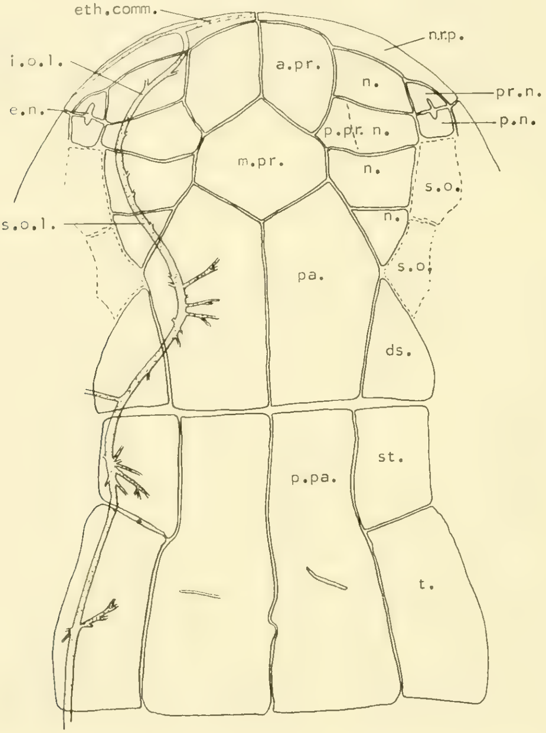


Fig. 1. *Ectosteorhachis.* Diagrammatic reconstruction of the dermal skull roof in dorsal view.

There is a pair of anterior postrostral bones and, posterior to these, a single median postrostral with, in some specimens, a pair of smaller postrostrals lying near its anterior margin, between the median postrostral and the second nasal element.

The infraorbital lateral line is borne upon the lachrymal and thence directly on to the naso-rostro-premaxilla. There are no separate lateral or anterior rostral elements associated with it. The single external narial aperture is bounded by two small bones which have been termed the prenarial and postnarial

(Westoll, 1943). The homology of these bones will be discussed in a later section.

Because of the extent of the postrostral bones, the parietal bones occupy a relatively short part of the roof of the ethmoid region. There is no external parietal foramen. The dermosphenotics, postparietals, supratemporals, and tabulars are arranged in the normal rhipidistian way (Fig. 1). The dorsal margin of the orbit seems to be formed by two supraorbitals on each side (Fig. 1, *s.o.*).

The cheek plate (Fig. 2A). The cheek plate in *Ectosteorhachis* is made up of lachrymal, jugal, postorbital and squamosal bones arranged in the normal rhipidistian manner.

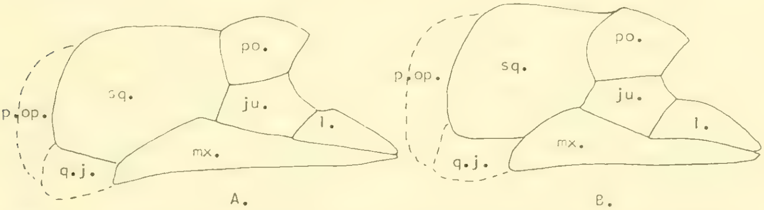


Fig. 2. Schematic reconstruction of the anterior cheek-plate region. A, *Ectosteorhachis,* B, *Megalichthys.*

The palate (Fig. 3A). I have only studied the ethmoid division of the palate. The only other rhipidistian in which the palate has been described in detail is *Eusthenopteron* (Jarvik, 1942, 1944, 1954), a rhizodontid. The palate of *Ectosteorhachis* differs significantly from that of *Eusthenopteron.* The vomers of *Ectosteorhachis* are almost triangular in shape and do not quite meet in the midline. Each vomer bears a pair of alternating tusks and an anterior ridge of marginal teeth. The parasphenoid seems to consist of two parts: the tooth-bearing ridge which reaches about halfway along the flat ventral surface of the endocranium, and a thin bony lamina which (as described by Romer, 1937) continues forward and lateral to the ridge. The whole is fused solidly to the endocranium. The palato-quadrate complex is exactly comparable, as far as I am able to tell, with that described by Watson (1926) in *Megalichthys.*

The conformation of the endocranial part of the palatal aspect of the ethmoid division of the skull is shown in Figure 3A. A major point of interest is the configuration of the anterior palatal recesses (Fig. 3A, *a.p.r.*). These are shallow pits lying between the anterior margin of the endocranium and the overlying dermal bones; they are separated from each other by posterior medial expansions of the premaxillary bones where each bone bears a stout tusk. When the lower jaws were occluded (as seen in specimen MCZ 9830), these anterior recesses served to receive the tips of a pair of large tusks at the anterior ends of the lower jaw rami (cf. Thomson, 1962).

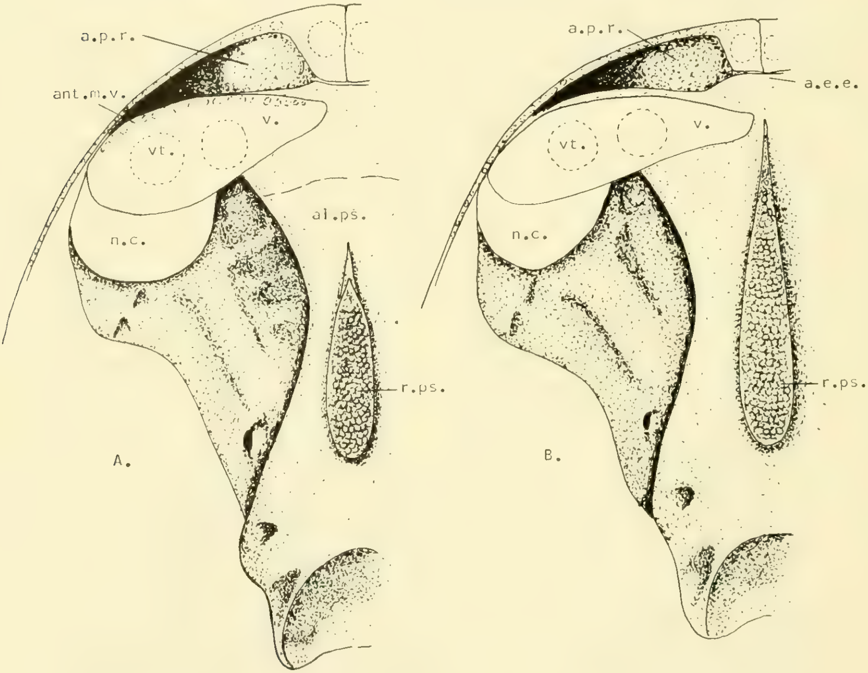


Fig. 3. Ethmoid region of the palate. Ventral view. A, *Ectosteorhachis*, B, *Megalichthys*.

The lower jaws (Fig. 4, A, B, C; based mainly on specimens MCZ 8641, 8826, 8827). As may be seen in Figure 4A, the outer aspect of the lower jaw does not differ greatly from that of *Megalichthys* (as figured by Watson, 1926). It is made up of the dentary and four infradentary elements — splenial, postsplenial, angular, and surangular. These elements are approximately demarked by grooves in the shiny continuous enamel covering on the dermal bones (Fig. 4A, *gr.*).

The inner surface of the lower jaw is made up of the following elements: dentary, three coronoids, prearticular and articular (Fig. 4, B, C). The dentary bone bears, at the anterior tip of the jaw, a large tusk, replaced in an alternating manner (Fig. 4, B, C, *d.t.*), and behind this a broad ridge — which I have termed the *crista dentalis* (Fig. 4, B, C, *cr.d.*). The crista dentalis is covered with small denticles and seemingly serves to occlude with a ridge of teeth on the anterior margin of the vomer. The crista dentalis is formed as an enlargement of the anterior rim of the anterior dentary fossa (Fig. 4B, *a.d.f.*) — a large pit for the reception of the vomerine tusks.

The prearticular covers a large part of the inner surface of the jaw (Fig. 4B, *pr.art.*) and also plays a large role in the formation of the jaw symphysis. A concave facet on each

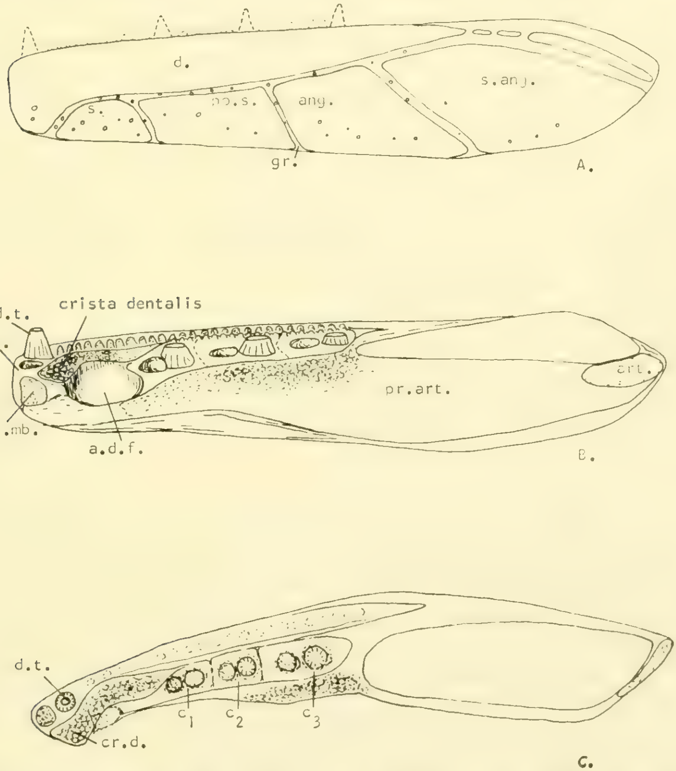


Fig. 4. *Ectosteorhachis.* Lower jaw. A, lateral view of the left ramus. B, inner view of right ramus. C, occlusal view of right ramus.

surface of the symphysial region (Fig. 4B, *s.mb.*) must have contained a small mental bone such as has been described in many Rhipidistia.

The gular series, as depicted by Hussakof (1911, fig. 53), comprises a pair of principal gulars, an anterior median gular, and on each side a row of six lateral gulars.

MEGALICHTHYS

Dermal skull roof. The dermal bones of the skull of *Megalichthys* have been described in part by many authors, but due to the problem of the coalescence of the outer layers of the dermal bones, many details, especially of the ethmoid region of the skull roof, have never been described. Miall (1884), Traquair (1884), Wellbourne (1900), Birks (1914), and Moy-Thomas (1935) have all added in some way to the original description of the skull by Agassiz (1843). Moy-Thomas' figure of the skull (1935, fig. 1) is the most complete restoration. Holmgren and Stensiö (1936, fig. 272 C) figured the anterior region of the snout of a specimen in the British Museum (Natural History), number P. 7875 (not P. 1878 as quoted by Holmgren and Stensiö), a new drawing of which is presented here (Fig. 6E). This specimen shows the arrangement of the dermal bones of the snout very well, since weathering of the fossil has exposed the sutures between the separate bones.

There is some variability in the arrangement of the smaller elements in the snout region of *Megalichthys.* Figure 6 shows the pattern of the dermal bones in six of the specimens (BMNH P. 7729, P. 7842, P. 7846, P. 7878, P. 7886, 21421) which have been used to derive what I consider to be the typical condition (Fig. 5).

The premaxillary unit is a naso-rostro-premaxilla, as in *Ectosteorhachis.* The supraorbital lateral line is carried from the parietal bone to the nasal area of the premaxilla by a row of nasal elements, of which five seems to be the typical number (cf. Pl. 1). Fusions of the nasals may occur (Fig. 6), most commonly between nasals 2 and 3, and nasals 4 and 5.

The most anterior of the nasal elements on each side is a large bone which might be interpreted as being fused with a more median anterior postrostral bone (Fig. 5, *n.pr.?*). There is a pair of posterior postrostral bones which may also merge with nearby nasals (Fig. 6F). In certain cases a median posterior postrostral bone may be present between the posterior postrostrals (Fig. 6F, *m.pr.*).

The infraorbital lateral line passes directly from the lachrymal to the naso-rostro-premaxilla and has no connection with the bones surrounding the external naris. The external naris is bounded by two bones, an anterior prenarial bone which is very large, and a smaller postnarial (Fig. 5, *pr.n.*, *p.n.*).

The parietals are relatively long, compared with *Ectosteorhachis;* they lack the external parietal foramen. With regard to the rest of the dermal skull roof I have been able to add little to Moy-Thomas' description (1935).

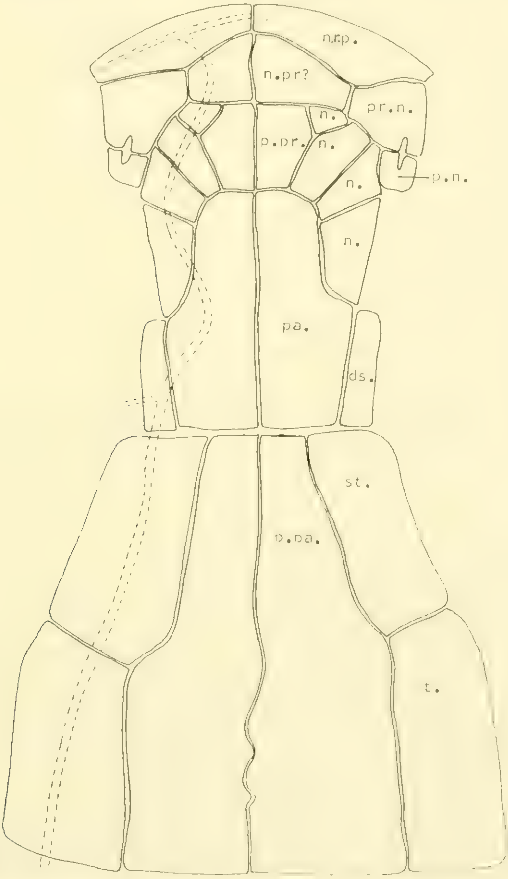


Fig. 5. *Megalichthys.* Diagrammatic reconstruction of the dermal skull roof in dorsal view.

The cheek region (Fig. 2B). The arrangement of the lachrymal, jugal, postorbital and squamosal bones in the cheek region is essentially similar to that of *Ectosteorhachis*.

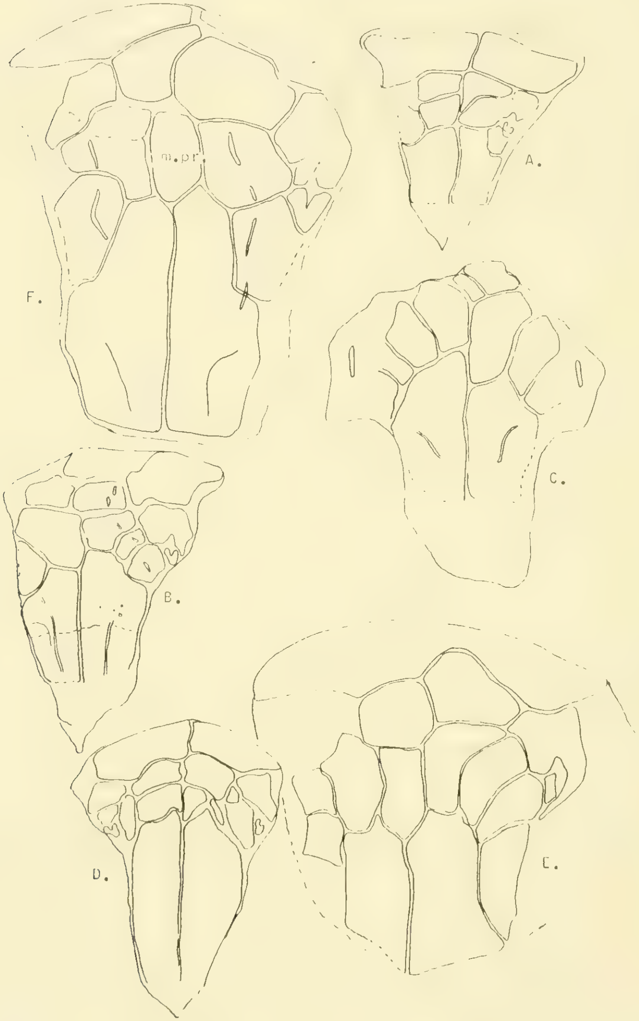


Fig. 6. A - F. *Megalichthys*. Sketches of six specimens showing arrangement of the dermal bones of the ethmoid division of the skull. Dorsal views. A, BMNH P. 7846; B, BMNH P. 7842; C, BMNH P. 7729; D, BMNH 21421; E, BMNH P. 7886; F, BMNH P. 7878.

The palate (Fig. 3B). The ethmoid region of the palate is remarkably similar to that of *Ectosteorhachis*. In *Megalichthys* the anterior palatal recess is also divided into two parts by the bases of the premaxillary tusks, and in addition, by a short anterior projection of the median segment of the anterior margin of the endocranium, which abuts against the premaxillae. (See Fig. 3B, *a.e.e.*)

The tooth-bearing ridge of the parasphenoid is long, reaching almost to the very tip of the endocranium. It has not been possible to establish whether or not there is an anterolateral extension of the parasphenoid corresponding to that of *Ectosteorhachis*. The vomers (Fig. 3B, *v.*) are of roughly triangular shape; they approach each other in the midline in the region of the tip of the parasphenoid. There is a pair of alternating tusks on each vomer; the anterior margin of the vomer is not strongly denticulate.

The lower jaws. The lower jaw of *Megalichthys* was described by Watson (1926, figs. 37, 38); a few very minor modifications must be noted. I have been able to confirm, from specimens (e.g. nos. P. 7886-7888 in the British Museum (Natural History), that there are three coronoid bones in *Megalichthys* (Watson had noted that the posterior of the two coronoids he figured might be double). The adductor fossa is rather wider, and the prearticular bone somewhat more narrow than is shown in Watson's figures. The crista dentalis is absent.

The gular series, as depicted by Moy-Thomas (1935, fig. 3) for example, consists of a pair of principal gulars, an anterior median gular, and six pairs of lateral gulars.

DISCUSSION

There can be no doubt that *Ectosteorhachis* and *Megalichthys* are closely related and have evolved either one from the other or together from the same (Devonian) osteolepid. Bystrov (1950) was of the opinion that *Megalichthys* is a direct descendant of *Osteolepis*. The principal purpose of this study is to set down the diagnostic differences between *Ectosteorhachis* and *Megalichthys*, but in order fully to understand the characteristic features of these fishes it will be necessary to refer to the Osteolepidae of the Devonian.

I have not been able to bring to light any significant differences in the patterns of the dermal bones of the posterior part of the skull roof between *Ectosteorhachis* and *Megalichthys*, although both differ from the other Osteolepidae in having only two extrascapular bones. There are very characteristic differences between the two genera in the pattern of the dermal bones of the ethmoid region — differences which, incidentally, help to clear up a twenty-year old confusion concerning the homology of the various bones in the narial region.

The composition of the naso-rostro-premaxilla seems to be the same in both *Ectosteorhachis* and *Megalichthys*. The nasal series is essentially the same in both genera; the number of separate nasal elements may be reduced by fusions, but there seem to have been, basically, five nasals, excluding the one incorporated into the premaxillary complex.

The parietal bones in *Megalichthys* are proportionately longer than in *Ectosteorhachis;* this seems to be associated with the corresponding increase in the size of the postrostral elements in the latter genus. The pattern of the postrostral elements seems to have been derived from that of a form such as *Osteolepis* (cf. Fig. 7A) in which there was but a single postrostral element situated between the rear nasals. In *Megalichthys* there is a pair of postrostrals in this position and the anterior nasal bones are enlarged mesially. In *Ectosteorhachis* the anterior nasal bones are small and lie lateral to a pair of anterior postrostrals which have the appearance (cf. Figs. 1 and 5) of having been divided off from the mesial part of the anterior nasals of a form like *Megalichthys*. Posterior to these, in *Ectosteorhachis*, there is a single, median and large posterior postrostral bone corresponding exactly with the single postrostral bone of *Osteolepis* (cf. Figs. 1 and 7A). The arrangements of these bones in *Ectosteorhachis* and *Megalichthys* would seem to indicate that these genera have evolved independently from a Devonian ancestor; however, the judgment of Westoll concerning such bones is that they are anamestic bones and therefore of limited phylogenetic significance.

In order to interpret the significance of the pattern of the bones around the external naris it is necessary to refer to the arrangement of these elements in *Osteolepis* (Fig. 7A), as it has been described by Jarvik (1948). In *Osteolepis* the external naris is bounded ventrally by a single element — the lateral rostral — which is a true rostral element (*sensu* Jarvik), containing a segment of the infraorbital lateral line in its passage from the lachrymal to the premaxilla. The external naris is bounded by two small dermal bones, sometimes fused into a single element, which are termed the anterior tectals. These three circumnarial bones fit in between the nasal series and the compound premaxilla. Posteriorly they are bounded by the lachrymal, which may slightly underly the lateral rostral, and the supraorbito-tectal, which lies between the posterior of the anterior tectals and the anterior of the two supraorbitals.

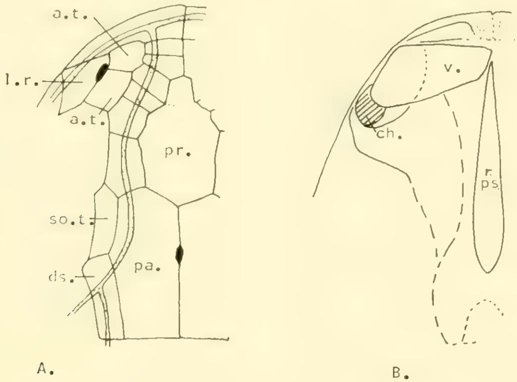


Fig. 7. A, Skull roof of *Osteolepis* (from Jarvik, 1948, fig. 16a). B, Restoration of the ethmoid division of the palate of a Devonian "osteolepid." (Composite of *Osteolepis* and *Glyptopomus.*)

The situation in the post-Devonian Osteolepidae is rather different. In *Megalichthys* the external naris is bounded by two elements — a larger prenarial and a smaller postnarial[1]. As shown in Figure 5, the larger prenarial bone bounds the narial opening in front and it extends both dorsally and ventrally of the naris. There is no connection of this bone with the lateral line system. The postnarial is small and bounds the naris posteriorly. The prenarial is bounded by the nasals, the naso-rostro-premaxilla, the postnarial and the lachrymal. The postnarial is bounded by the nasals, the anterior supraorbito-tectal, the lachrymal and the prenarial. The lachrymal bone makes contact with the premaxilla, and the infraorbital lateral line passes directly between these bones.

[1] It should be noted that Westoll's figures of the snout of *Megalichthys* (1943, fig. 8, c and d), showing prenarial and postnarials of equal size, seem to have been restored after the condition in *Ectosteorhachis*.

In *Ectosteorhachis* the narial aperture is bounded by prenarial and postnarial bones having exactly the same relations to the other bones of the ethmoid region as in *Megalichthys*. The prenarial bone, however, is a small bone of the same size as the postnarial. The small size of the prenarials seems to be compensated for by the large size of the anterior postrostral bones which are not present in *Megalichthys*.

There is some confusion in the literature concerning the homology of these circumnarial elements. Jarvik considers the situation in *Osteolepis* to be primitive and has also concluded from his studies that the lateral rostral bone of this form corresponds to the septomaxilla of the tetrapods (1942). Westoll, on the other hand, has considered the situation in *Megalichthys* and *Ectosteorhachis*, with pre- and postnarial bones, to be primitive. He believes that the postnarial bone, which he states to be typically present in all Rhipidistia (1943, p. 90), is the homologue of the tetrapod septomaxilla. Westoll also considered that the lateral rostral bone of Devonian Osteolepidae and Rhizodontidae did not have a primary relationship with the infraorbital lateral line canal.

All the evidence that I have collected during this study seems to indicate that *Megalichthys* and *Ectosteorhachis* have evolved from typical Devonian Osteolepidae, and the nature of the circumnarial bones serves only to emphasize this view. The position, shape and size of the prenarial bone of *Megalichthys* indicate that this element has been formed from the merging of a lateral rostral and the more anterior member of a pair of anterior tectals of a form such as *Osteolepis*, so that the "new" element encloses the naris from in front. In *Ectosteorhachis* the prenarial is small and we may suppose the decrease in size as compared with *Megalichthys* is associated with a reduction of the anterior tectal component of the prenarial bone. The nature of the prenarial bone in *Ectosteorhachis* may thus be interpreted as evidence suggesting that this genus has been evolved from *Megalichthys* itself.

The postnarial bone in both *Megalichthys* and *Ectosteorhachis* seems to correspond to the more posterior of the anterior tectals of a form such as *Osteolepis*, which, with the shifting forwards of the lateral rostral element, has moved ventrally to enclose the naris from behind.

Although the arrangement of the circumnarial bones in *Megalichthys* and *Ectosteorhachis* may thus be considered to have been secondarily derived from that of Devonian forms, the name "prenarial" (Westoll, 1943) must be retained for these two genera since it would be inaccurate to consider this element to represent solely the lateral rostral bone. Similarly the name "postnarial" is to be preferred to "anterior tectal" since this bone does not have the same relations with the surrounding bones as it does in the Devonian Osteolepidae.

The supraorbital series was rarely preserved in the material available to me, but seems to have consisted of two elements as in most Rhipidistia (cf. Westoll, 1943).

The cheek region. As shown in Figure 2, the anterior part of the cheek region is essentially the same in both genera. The maxilla and squamosal are slightly longer in *Ectosteorhachis* than in *Megalichthys.*

The palate. The ethmoid division of the palate is very similar in the two genera (see Figure 3). Division of the anterior palatal recess into two portions is effected by an expanded part of the premaxilla on either side of the midline in *Ectosteorhachis.* In *Megalichthys* there is, in addition, a short "buttress" from the anterior part of the endocranium.

The tooth-bearing part of the parasphenoid is much longer in *Megalichthys* than in *Ectosteorhachis.* In the former genus it reaches to the anterior tip of the endocranium and touches the median extremities of the vomers. In *Ectosteorhachis* the tooth-bearing ridge of the parasphenoid ends far posteriorly and there is no contact with the vomers.

The anterior rim of the vomers in *Ectosteorhachis* is more prominently toothed than in *Megalichthys.*

The lower jaws. There is little difference to be observed between the two genera with respect to the outer surface of the lower jaw rami. In *Ectosteorhachis* the grooves in the outer surface of the enamel contain "pit-organs" which are lacking in *Megalichthys.*

With respect to the inner surface of the lower jaw rami, there are greater differences between the two genera. The adductor fossa is longer and a little wider in *Ectosteorhachis* than in *Megalichthys* (in the former the adductor fossa takes up about four-tenths of the total length of the jaw; in *Megalichthys* about three-tenths). The crista dentalis, present in *Ectosteorhachis,* is lacking in *Megalichthys.*

Comparison with other Osteolepidae. We have seen above that the pattern of the dermal bones of the snout of *Ectosteorhachis* and *Megalichthys* (the only non-Devonian members of the family Osteolepidae) may readily be derived from that of a form such as *Osteolepis;* unfortunately the other Devonian members of this family are less well known (cf. Jarvik, 1948, 1950).

The palate of *Glyptopomus* as revealed in dorsal view only, has been described by Jarvik (1950, fig. 6). By combining details from this description and from specimens of *Osteolepis* in the Museum of Comparative Zoology (nos. MCZ 8737, 5875), I have been able to derive a highly tentative reconstruction of the ventral surface of the palate of an hypothetical generalised Devonian "osteolepid" (Fig. 7B). The vomers are of the roughly triangular shape seen in the later forms, and have a slightly wider region of contact in the midline. The tooth-bearing ridge of the parasphenoid is very long and thin, extending along the whole length of the ethmoid endocranium. It is interesting to note the progressive shortening and broadening of the tooth-bearing ridge in the sequence "Devonian osteolepid" to *Megalichthys* to *Ectosteorhachis.*

The crista dentalis seems to be a specialised feature of *Ectosteorhachis.* The only other genera in which it has been reported are *Panderichthys* (Gross, 1941, fig. 22), which has a few small denticles in this position, and *Litoptychius* (Denison, 1951, fig. 46), which, although it has been described as a rhizodontid[1], may thus have features in common with the Osteolepidae.

CONCLUSIONS

The results of this study have been to show that the Permian rhipidistian of North America known as *Ectosteorhachis* is generically distinct from the Carboniferous genus known as *Megalichthys* which occurs in both Europe and North America. The two genera are very closely related to one another and the evidence of the circumnarial bones in the snout seems to demonstrate that *Megalichthys* evolved from a Devonian osteolepid and that the genus *Ectosteorhachis* separated from *Megalichthys* at a later date. The evidence from the postrostral bones might be interpreted as indicating that the separation between *Megalichthys* and *Ectosteorhachis* occurred before the pattern of these elements had become stabilised; but this is not borne out by the temporal distribution of the fossils. The genus *Megalichthys* occurs in the Carboniferous of both Europe and North America, but *Ectosteorhachis* has only been found in the Lower Permian of North America.

---

[1] Denison described *Litoptychius* as a member of the family Rhizodontidae, but Orvig (1957) expressed the opinion that it is a member of the Holoptychidae (basing his argument on the structure of the scales). However, the symphysial region of the lower jaw of *Litoptychius* lacks the parasymphysial tooth whorls which are now (Jarvik, 1962) said to be typical of the Holoptychidae and Porolepidae.

In partial summary of the anatomical evidence discussed in the preceding pages, I present amended generic diagnoses of *Megalichthys* and *Ectosteorhachis*.

Order CROSSOPTERYGII Cope, 1872

Suborder RHIPIDISTIA Cope, 1887

Family OSTEOLEPIDAE Smith-Woodward, 1891

Genus MEGALICHTHYS Agassiz, 1843

Type species: Megalichthys hibberti Agassiz, 1843.

To the list of synonyms given by Smith-Woodward (1891) must be added:

Parabatrachus Owen, 1853: Hay, 1902, p. 362; Berg, 1958, p. 92.

Carlukeus Whitley, 1940, p. 242.

Occurrence: Carboniferous of Europe and North America.

Amended diagnosis (cf. Smith-Woodward, 1891): Dermal bones of the skull arranged as in *Osteolepis* with the following exceptions. The external naris is surrounded by a very large prenarial bone and a smaller postnarial bone. The lateral rostral bone is not present as an independent unit and the infraorbital lateral line canal passes directly from the lachrymal bone to the premaxilla. There are no independent anterior postrostral bones; the posterior postrostral is paired. There is no parietal foramen. There are two extrascapulars. The vomers are triangular in shape and bear two tusks replacing each other alternately. The anterior margin of the vomer is not prominently toothed. The tooth-bearing ridge of the parasphenoid reaches as far anteriorly as to touch the median tips of the vomers. All teeth are rounded in cross-section.

The vertebrae are ossified as narrow rings and the neural and haemal arches are fully developed.

The scales are more or less smooth and punctate. The tail is heterocercal, tending towards diphycercal. The pectoral fins are set rather far back; their bases are covered with scales, as are those of the pelvic fins. The anterior dorsal fin is set slightly in advance of the pelvic fins and the posterior dorsal fin opposes the anal fin.

MEGALICHTHYS HIBBERTI Agassiz, 1843

Lectotype (here selected[1]): BMNH no. P. 42516. Skull and partial trunk.

Comments: I have no new information to add to Smith-Woodward's diagnosis (1891) of this species.

Genus ECTOSTEORHACHIS Cope, 1880

Type species: Ectosteorhachis nitidus Cope, 1880.

Previous authors have thought that this genus is a synonym of the following:

Megalichthys Agassiz, 1843: Cope, 1891, p. 457; Hussakof, 1911, p. 168.

Parabatrachus Owen, 1853: Hay, 1899, p. 788; Hay, 1902, p. 362; Berg, 1958, p. 92.

Occurrence: Lower Permian of North America.

Amended diagnosis (cf. Hussakof, 1911): Dermal bones of the skull arranged in the manner of *Osteolepis*, with the following exceptions. The naris is surrounded by prenarial and postnarial bones of equal size. There is no separate lateral rostral bone and the infraorbital lateral line passes directly from the lachrymal to the compound premaxilla. There is a pair of anterior postrostral bones and a single, large, median posterior postrostral bone. There are two extrascapulars. The vomers are triangular with a pair of alternating tusks. The anterior margin of the vomer is prominently toothed. The tooth-bearing ridge of the parasphenoid does not reach so far anteriorly as to meet the median tips of the vomers, but ends at the level of the posterior wall of the nasal capsule.

The dentary bone of the lower jaw overlaps the prearticular bone in the symphysial region, as a denticulate ledge — the crista dentalis.

The scales are smooth and punctate. The tail is intermediate between the heterocercal and diphycercal conditions. The pectoral fins are set rather far back. The anterior dorsal fin is inserted in advance of the pelvic fins and the posterior dorsal fin opposes the anal fin.

---

[1] See below, discussion of nomenclature.

ECTOSTEORHACHIS NITIDUS Cope, 1880

Type: AMNH no. 7239. Skull and anterior scales.

Diagnosis: As for the genus. This is the only known species of *Ectosteorhachis.*

THE NOMENCLATURE OF *MEGALICHTHYS*

The history of the nomenclature of the genus *Megalichthys* is rather complicated. The genus was named by Agassiz in a paper (Hibbert, 1835b) published by Hibbert in 1835[1] for remains of a large "sauroid" fish that had been discovered in the Carboniferous limestone quarry at Burdiehouse near Edinburgh. The remains of this "large fish" had been previously mentioned in various contexts (such as the report of Hibbert to the Geological Section of the British Association for the Advancement of Science, in 1834 [published 1835], and in Agassiz's address to the same meetings). But these instances do not constitute definite "indication" in the sense of the 1961 International Code of Zoological Nomenclature. Hibbert's was the first scientific account and the first proper description.

The remains consisted of some large teeth, some smaller teeth, and scales of assorted sizes. These specimens had been shown, during the 1834 British Association meetings, to Agassiz who was then in Great Britain collecting material for his "Poissons Fossiles." At the time there was a controversy in scientific circles about whether such remains were *sauroid* (i.e. resembling reptiles) or *saurian* (actually pertaining to reptiles). Agassiz and Buckland decided to settle the matter and, subsequently visiting various public museums in England, they found in the Leeds Museum a rather complete head and part of the trunk[2] of a sauroid fish from the Yorkshire coalfields. This, they decided, was identical with the Burdiehouse material. The problem of the *nature* of the Burdiehouse remains was thus solved and ". . . after M. Agassiz had . . . established that these teeth and certain other osseous remains of Burdiehouse belonged to a sauroid fish . . . he considered it as a new genus to which he gave the name of *Megalichthys;* and to the species found at Burdiehouse he added the name of *Megalichthys hibberti.*" (Hibbert, 1835b, p. 202.)

---

[1] Volume 13 of the Transactions of the Royal Society of Edinburgh, where the paper appeared, was issued between 1834 and 1836. Hibbert's paper (according to Neave, 1940) was published in February 1835. Most authors (e.g. Smith-Woodward, 1891) have given the date as 1836.

[2] Now in the British Museum (Natural History) No. P. 42516.

Fleming in October 1835 described some remains[1] of *Megalichthys hibberti*[2] under the name of *Ichthyolithus clackmanensis.*

In 1837 Sir Philip Grey Egerton, in a revised catalogue of the collections of himself and Lord Cole, uses the name *Holoptychius hibberti* in addition to the name *Megalichthys hibbertii*[3] for specimens in his possession from Burdiehouse. Egerton cites "Agassiz mss" as his authority for the former name. Also in 1837, Buckland uses the names *Holoptychus*[4] and *Megalichthys* and the authority for this, although not stated, was probably also "Agassiz mss" since most of Agassiz's friends in Britain seem to have had access to Agassiz's notes and intentions in advance of publication.

Buckland, however, has confused the picture somewhat: in the text of his work (1837, vol. 1, p. 275) he states that "plate 27, figures 11, 12, 13, 14, represent teeth from . . . the fishes . . . referred by M. Agassiz to a new genus *Megalichthys.*" In the explanation of the plates appearing in volume two of the same work Buckland states that "plate 27, figures 11, 13, 14" are *Holoptychus (sic) hibberti* and "figure 12" is *Megalichthys hibberti* (p. 43). The acknowledged source of the figures is Hibbert's (1835) treatise.

Whatever the reason for this confusion, and regardless of what Buckland actually intended to state, the fact remains that someone, probably Agassiz himself, had recognised that the Burdiehouse remains represented two different fishes. In 1840 Owen made this distinction formal by applying to the larger teeth from Burdiehouse the new generic name *Rhizodus.* But Owen states that the new genus *Rhizodus* is named to replace *Holoptychius hibberti* Agassiz, and presumably, since Owen did not name a type species of *Rhizodus*, he assumed it would simply take over the specific name of "*Holoptychius*" *hibberti* Agassiz. Unfortunately, Owen's authority for the latter name must have been an unpublished Agassiz manuscript for the name does not appear in "Poissons Fossiles" until 1843, when Agassiz merely cites the name, in a list, as "*Holoptychius hibberti* Owen *(Rhizodus)*, Burdiehouse." The specimens concerned are the large teeth and scales from Burdiehouse (figured by Hibbert and Buckland, see Table 1) as well as the specimen figured by Owen (locality unknown).

---

[1] Now in the Royal Scottish Museum, Edinburgh, No. 1950.38.58.

[2] "*Megalichthys*" in the sense of this paper.

[3] The spelling of the specific name *hibberti* or *hibbertii* seems to have varied with the preference of the author.

[4] Apparently a misprint for *Holoptychius.*

Agassiz finally (1843) described the "Leeds Head" specimen, as it has become known (and other material which he considered to belong to the species *M. falcatus*), but he did not mention whether or not he still considerd any of the Burdiehouse material to belong to the genus *Megalichthys*. In fact he states only that the localities of *Megalichthys* are numerous, "on en a découvert dans le pays de Galles, dans les environs de Manchester, près de Stafford et dans les environs de Glasgow." This list may by no means be considered complete, since the actual specimen Agassiz was describing came from Yorkshire.

In 1853 Owen described as a new amphibian, *Parabatrachus colei*, a specimen which later (Young, 1868) was shown to be the maxilla of *Megalichthys hibberti* (*sensu* Agassiz).

M'Coy (1855) seems to have been the first to realize the anomaly in the nomenclature of *Rhizodus* and *Megalichthys*. He noted that, in disregard of the facts of the case, the "Leeds head" was considered to be the type of *Megalichthys hibberti* and the Burdiehouse specimens were considered to belong to *Rhizodus hibberti*. M'Coy decided "against my better judgment" to "leave it as it is."

There is little doubt that the name *Megalichthys* was originally intended to describe the "big-fish" of Burdiehouse which is now known as *Rhizodus*. However, there is similarly no doubt that when Hibbert used the name *Megalichthys hibberti* he meant it to apply to the Burdiehouse remains — the "teeth and certain other osseous remains" mentioned above, and these remains, which included both "*Rhizodus*" and "*Megalichthys*" were the true types of *Megalichthys hibberti* Agassiz *in* Hibbert 1835.

Thus Traquair (1884) noted that the Burdiehouse material[1] still remaining in the genus *Megalichthys* has priority concerning the specific name *hibberti*, but, having concluded that the Burdiehouse remains of *Megalichthys* are "different specifically" from the "Leeds head" specimen, and acquiescing to the popular conception that the latter forms the type specimen of *Megalichthys hibberti*, he described the Burdiehouse *Megalichthys* with the aid of new material collected there by Hugh Miller, as the new species *Megalichthys laticeps*.

---

[1] "Scales and bones . . . actually figured under that name (*M. hibberti*) *along with* (my italics, KST) remains of *Rhizodus* by Dr. Hibbert" (Traquair, 1884, p. 118).

The position taken by M'Coy and Traquair has been accepted by Smith-Woodward in his "Catalogue of Fossil Fishes" and by many subsequent authors (not, however, by all, see Hay, 1902; Jordan, 1923; Berg, 1958).

There seems no merit in proposing that *Rhizodus hibberti* Owen be renamed *Megalichthys hibberti* Agassiz *in* Hibbert 1835; similarly there seems no merit in the proposition that the genus now known as *Megalichthys* Agassiz 1843 be renamed *Parabatrachus* Owen 1853, with type species *clackmanensis* Fleming 1835. The common usage has remained unchanged since at least 1855, and has been adopted by no less authorities than Agassiz himself and Smith-Woodward. I propose, therefore, to invoke Rule 23b of the International Code of Zoological Nomenclature, and formally to request the Commission to stabilise the *status quo* of Smith-Woodward's "Catalogue" (volume 2, 1891) on the subject. I propose that the "Leeds head" (BMNH no. P. 42516) be adopted as the lectotype of *Megalichthys hibberti* Agassiz 1843, and that the large mandibular tooth figured by Hibbert (1835b, pl. 9, fig. 2) now in the Royal Scottish Museum (no. 1950.38.63) be adopted as the lectotype of *Rhizodus hibberti* Owen 1840, in place of the specimen originally figured by Owen and which is now lost.

As a summary of the history of the nomenclature of the Burdiehouse specimens, I have drawn up the following table:

Table 1

The Burdiehouse specimens

All originally described by Hibbert (1835, pl. 8, figs. 1 to 6, pl. 9, figs. 1 to 10, pl. 10, figs. 1 to 3, pl. 11, figs. 2 to 8) as *Megalichthys hibberti* Agassiz.

now known as *Rhizodus*	now known as *Megalichthys*
1. Egerton (1837) from Agassiz MS "*Holoptychius hibberti*"	Egerton (1837) from Agassiz (1835) "*Megalichthys hibbertii*"
2. Buckland (1837, pl. 27, figs. 11, 13, 14, from Hibbert, 1835, pl. 9, figs. 2, 3 and 8) as "*Holoptychus hibberti*"	Buckland (1837, pl. 27, fig. 12 from Hibbert, 1835, pl. 9, fig. 10) as "*Megalichthys hibberti*"
3. Agassiz (1843) as "*Holoptychius hibberti* Owen, *(Rhizodus)*"	Agassiz (1843) as "*Megalichthys*"
4. M'Coy (1855) as "*Rhizodus hibberti*"	M'Coy (1855) as "*Rhizodus hibberti*"
5.	Traquair (1884), actual specimens not cited. Renamed "*Megalichthys laticeps*"
6. Smith-Woodward (1891) lists Hibbert's pl. 8, fig. 1, pl. 9, figs. 2, 3, 9, 10, as "*Rhizodus hibberti*"; Hibbert's pl. 8, fig. 2 as "*Rhizodus ornatus*"	Smith-Woodward (1891) lists Hibbert's pl. 11, figs. 2 to 8, as "*Megalichthys laticeps*"

LITERATURE CITED

AGASSIZ, J. L. R.

1835. On the fossil fishes of Scotland. Rep. Brit. Assoc. Adv. Sci., Edinburgh, **4:** 646-647.

1843. Récherches sur les poissons fossiles. Neuchatel and Soleure, vol. 2, 310 pp.

BERG, L. S.

1958. System der rezenten und fossilen Fischartigen und Fische. Deutscher Verlag, Berlin, 310 pp.

BIRKS, S. G.

1914. *Megalichthys:* a study incorporating the results of work on previously undescribed material. Trans. Nat. Hist. Soc. Northumberland Durham Newcastle, (n.s.) **4:** 307-329.

BUCKLAND, W.

1837. Geology and mineralogy considered with reference to natural theology. 1st ed. London, 2 vols., 552 pp.

BYSTROV, A. P.

1950. Microscopic structure of the bones and teeth of the Carboniferous crossopterygian fish *Megalichthys* (family Osteolepidae). Dokl. Akad. Nauk. U.S.S.R., **34:** 119-121. (In Russian.)

COPE, E. D.

1880. Second contribution to the history of the Vertebrata of the Permian formation of Texas. Proc. Am. Phil. Soc., **19:** 38-58.

1883. Fourth contribution to the history of the Permian formation of Texas. Proc. Am. Phil. Soc., **20:** 628-636.

1891. On the character of some Palaeozoic fishes. Proc. U.S. Nat. Mus., **14:** 447-463.

COPE, E. D. and W. D. MATTHEW

1915. Hitherto unpublished plates of Tertiary Mammalia and Permian Vertebrata. Am. Mus. Nat. Hist., Monograph series, 2.

DENISON, R. H.

1951. Late Devonian fresh-water fishes from the Western United States. Fieldiana, Geology, **11** (5): 221-260.

EGERTON, P. DE M. G.

1837. A systematic and stratigraphic catalogue of the fossil fishes in the cabinets of Lord Cole and Sir Philip Egerton; together with an alphabetical and stratigraphical catalogue of the same species, with reference to their published figures and descriptions. Rev. ed., London, 20 pp.

FLEMING, J.

1835. Notice of the remains of a fish found in connection with a bed of coal at Clackmannan. Edinburgh New Philos. Jour., **19:** 314-316.

GROSS, W.

1941. Über den Unterkiefer einiger devonischer Crossopterygier. Abh. Preuss. Akad. Wiss., math.-nat. Kl., **7:** 1-51.

HAY, O. P.

1899. On some changes in the names, generic and specific, of certain fossil fishes. Amer. Natural., **33:** 783-792.

1902. Bibliography and catalogue of the fossil Vertebrata of North America. Bull. U.S. Geol. Surv., **179:** 1-868.

HIBBERT, S.

1835a. On the ossiferous beds contained in the basins of the Forth, the Clyde, and the Tay. Rep. Brit. Assoc. Adv. Sci., Edinburgh, **4:** 642-644.

1835b. On the freshwater limestone of Burdiehouse, in the neighbourhood of Edinburgh, belonging to the Carboniferous group of rocks. With supplementary notes on other freshwater limestones. Trans. Roy. Soc. Edinburgh, **13:** 169-282.

HOLMGREN, N. and E. A. STENSIÖ

1936. Kranium und Visceralskelett der Akranier, Cyclostomen und Fische. *In:* L. Bolk, *et alia,* Handbuch der vergleichenden Anatomie der Wirbeltiere, vol. 4: 345-353.

HUSSAKOF, L.

1911. The Permian fishes of North America. Carnegie Institute Publ. no. 146: 153-178.

JARVIK, E.

1942. On the structure of the snout of crossopterygians and lower gnathostomes in general. Zool. Bidrag., **21:** 237-675.

1944. On the dermal bones, sensory canals and pitlines of the skull in *Eusthenopteron foordi* Whiteaves, with some remarks on *E. save-soderberghi* Jarvik. K. Svenska Vetens.-Akad. Handl., (3) **21:** 1-48.

1948. On the morphology and taxonomy of the Middle Devonian osteolepid fishes of Scotland. K. Svenska Vetens.-Akad. Handl., (3) **25:** 1-301.

1950. On some osteolepiform crossopterygians from the Upper Old Red Sandstone of Scotland. K. Svenska Vetens.-Akad. Handl., (4) **2:** 1-35.

1954. On the visceral skeleton in *Eusthenopteron* with a discussion of the palato-quadrate in fishes. K. Svenska Vetens.-Akad. Handl., (4) **5:** 1-104.

1962. Les Porolépiformes et l'origine des urodèles. Colloques Internat. du Centre National de la Récherche Scientifique, Paris, no. 104: 87-101.

JORDAN, D. S.

1923. A classification of fishes. Stanford Univ. Publ. Univ. Biol. Sci., **3** (2): 77-243.

M'COY, F.

1855. Systematic description of the British Palaeozoic fossils. *In:* Sedgwick and M'Coy, The British Palaeozoic Rocks and Fossils. Cambridge, 661 pp.

MIALL, L. C.

1884. On a new specimen of *Megalichthys* from the Yorkshire coal field. Quart. Jour. Geol. Soc. London, **40:** 347-352.

MOY-THOMAS, J. A.

1935. Notes on the types of fossil fishes in the Leeds City Museum. I and II. Acanthodii, Dipnoi, Crossopterygii and Elasmobranchii. Proc. Leeds Lit. Phil. Soc. (Sci. Sect.), **3:** 111-116.

NEAVE, S. A.

1940. Nomenclator Zoologicus. Vol. 3. Zool. Soc. London.

ϕRVIG, T.

1957. Remarks on the vertebrate fauna of the lower Upper Devonian of Escuminac Bay, P.Q., Canada, with special reference to the porolepiform crossopterygians. Arkiv. Zool., **10** (6): 367-426.

OWEN, R.

1840-1845. Odontography. London, 2 vols., 655 pp.

1853. Notice of a batrachoid fossil in British coal shale. Quart. Jour. Geol. Soc. London, **9:** 67-70.

ROMER, A. S.

1937. The braincase of the Carboniferous crossopterygian *Megalichthys nitidus*. Bull. Mus. Comp. Zool., **82** (1): 1-67.

1941. Notes on the crossopterygian hyomandibular and braincase. Jour. Morph., **69** (1): 141-160.

SMITH-WOODWARD, A. S.

1891. Catalogue of the fossil fishes in the British Museum. Part 2. London, 567 pp.

THOMSON, K. S.

1962. Rhipidistian classification in relation to the origin of the tetrapods. Breviora, Mus. Comp. Zool., no. 177: 1-12.

TRAQUAIR, R. H.

1884. Remarks on the genus *Megalichthys* Agassiz, with description of a new species. Geol. Mag., (3) **1:** 115-121.

WATSON, D. M. S.

1926. The evolution and origin of the Amphibia. Phil. Trans. Roy. Soc. London, (B) **214:** 169-257.

WELLBOURNE, E. D.

1900. On the genus *Megalichthys* Agassiz, its history, systematic position, and structure. Proc. Yorks. Geol. Soc., **14:** 52-71.

WESTOLL, T. S.

1936. On the structures of the dermal ethmoid shield of *Osteolepis*. Geol. Mag., **73:** 157-170.

1937. On a specimen of *Eusthenopteron* from the Old Red Sandstone of Scotland. Geol. Mag., **74:** 507-524.

1943. The origin of the tetrapods. Biol. Rev., **18:** 78-98.

WHITLEY, G.

1940. The Nomenclator Zoologicus and some new fish names. Austr. Nat., **10:** 241-243.

YOUNG, J.
1868. On the so-called labyrinthodont, *Parabatrachus* (Owen). Trans. Nat. Hist. Soc. Glasgow, (n.s.) **1:** 174-176.

(Received May 10, 1963)

ABBREVIATIONS USED IN THE ILLUSTRATIONS

a.d.f.	anterior dentary fossa
a.e.e.	anterior extension of the endocranium
ang.	angular
al.ps.	anterior lamina of parasphenoid
ant.m.v.	anterior margin of vomer
a.p.r.	anterior palatal recess
a.pr.	anterior postrostral
art.	articular
a.t.	anterior tectal
c_{1-3}	coronoids
ch.	choana
cr.d.	crista dentalis
d.	dentary
ds.	dermosphenotic
d.t.	dentary tusk
e.n.	external naris
eth.comm.	ethmoid commissure of lateral line system
gr.	groove in surface of lower jaw
i.o.l.	infraorbital lateral line
ju.	jugal
l.	lachrymal
l.r.	lateral rostral
m.pr.	median postrostral
mx.	maxilla
n.	nasal
n.c.	nasal cavity
n.pr?	possible united nasal and postrostral
n.r.p.	naso-rostro-premaxilla
pa.	parietal
p.n.	postnarial
po.	postorbital
p.op.	preopercular
po.s.	postsplenial
p.pa.	postparietal
p.pr.	posterior postrostral
p.pr.n.	posterior postrostral united with nasal
pr.	postrostral
pr. art.	prearticular

pr.n.	prenarial
ps.	parasphenoid
q.j.	quadrato-jugal
r.ps.	median ridge of parasphenoid
s.	splenial
s.ang.	surangular
s.mb.	symphysial mental bone
s.o.	supraorbital
s.o.l.	supraorbital lateral line
so.t.	supraorbito-tectal
sq.	squamosal
st.	supratemporal
t.	tabular
v.	vomer
vt.	vomerine tusk

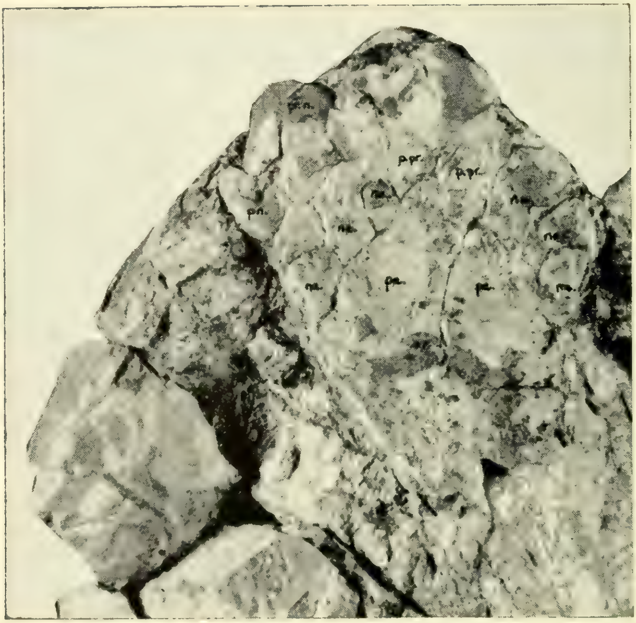

pr.n.
p.pr.
p.pr.
na.
pn.
na.
na.
na.
na.
pa.
pa.
pn.

Plate 1. *Megalichthys macropomus* Cope. MCZ 5143. Leavenworth Coal; Lansing, Kansas. Dorsal view showing dermal bones of ethmoid division of skull roof. Abbreviations: *na.*, nasal; *pa.*, parietal; *pn.*, postnarial; *p.pr.*, posterior postrostral; *pr.n.*, prenarial.

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 10

THE COMPARATIVE ANATOMY OF THE SNOUT IN RHIPIDISTIAN FISHES

By Keith Stewart Thomson

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
August 12, 1964

PUBLICATIONS ISSUED BY OR IN CONNECTION WITH THE

MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

BULLETIN (octavo) 1863 — The current volume is Vol. 131.

BREVIORA (octavo) 1952 — No. 207 is current.

MEMOIRS (quarto) 1864–1938 — Publication terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 41 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 28 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained from the Publications Office of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Peters' Check-List of Birds of the World. Volumes 1, 4 and 6 are out of print; volumes 2, 3, 5, 7, 9, 10 and 15 are currently available.

Phylogeny and Evolution of Crustacea. Proceedings of a conference held at Cambridge, Mass., March 6-8, 1962. H. B. Whittington and W. D. I. Rolfe, editors. Cambridge, Mass., 192 pp., 80 figs., 1963. Cloth bound, $6.75.

Fishes of the Gulf of Maine, by Henry B. Bigelow and William C. Schroeder. Washington, viii - 577 pp., 1953. Photo-offset reprint, $6.50.

PUBLICATIONS OF THE BOSTON SOCIETY OF NATURAL HISTORY

The remaining stock of the scientific periodicals of the Boston Society of Natural History has been transferred to the Museum of Comparative Zoology for distribution. Prices for individual numbers may be had upon request.

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 10

THE COMPARATIVE ANATOMY OF THE SNOUT IN RHIPIDISTIAN FISHES

By Keith Stewart Thomson

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
August, 1964

Bull. Mus. Comp. Zool., Harvard Univ., 131(10):313-357, August, 1964

No. 10 — *The comparative anatomy of the snout in rhipidistian fishes*

By Keith Stewart Thomson[1]

INTRODUCTION

Due mainly to the work of Goodrich and Gregory it is now almost universally accepted that the Rhipidistia (fossil fishes of the order Crossopterygii, in the system of Romer, 1955) are the closest ancestors of the tetrapods. In general it has been assumed that the first tetrapods, the Amphibia, were of monophyletic origin, but certain theories of a diphyletic origin have been proposed. It has been argued that, of the living Amphibia, the Urodela and Anura represent two distinct lineages. Also, while the fossil history of the Recent Amphibia is very incomplete, it has been noted that the two major groups of Palaeozoic amphibians, the Apsidospondyli and the Lepospondyli, have yet to be shown to have a common ancestor. Both Säve-Söderbergh and Holmgren proposed a diphyletic theory whereby the Dipnoi were stated to be the ancestors of the Urodela and the Rhipidistia the ancestors of the Anura. This theory is not now generally accepted. A second diphyletic theory is that of Jarvik (1942) who, while rejecting the Dipnoi as possible ancestors, proposed that the Urodela and Anura arose from separate stocks of Rhipidistia. It is with this theory that the present investigation is concerned.

From a study of the snout anatomy of the Rhipidistia and a review of the anatomy of the snout in other gnathostomes, Jarvik (1942) concluded that the Rhipidistia comprise two separate stocks—the "Porolepiformes" (families Porolepidae and Holoptychidae) and the "Osteolepiformes" (family Osteolepidae and Rhizodontidae). Jarvik studied the Lower Devonian genus *Porolepis* as his type of the "Porolepiformes" and the Upper Devonian rhizodontid genus *Eusthenopteron* as his type of the "Osteolepiformes." He gives a detailed account of the snout anatomy of these two forms and of the differences between them. He considers that the differences he observed indicate a basic split in the Rhipidistia. Further studies (1962) have elaborated this theory.

Jarvik claims that the two groups of Rhipidistia gave rise independently to tetrapod vertebrates — the "Porolepiformes" to the Urodela, and the "Osteolepiformes" to the Anura and probably to all other vertebrates. Jarvik's evidence for this is that from an extensive review of the snout anatomy in certain Amphibia he concluded not only that the Urodela were fundamentally different from the Anura, but that the diagnostic features of distinction between the two "types" of snout anatomy could be identified in the two "stocks" of Rhipidistia also. Thus he believes that the supposedly "characteristic" natures of the snouts of "porolepiform" and "osteolepiform" rhipidistians have survived essentially unchanged in the Recent amphibians.

---

[1] Present address: Department of Zoology, University College London.

In general there has been hesitation in accepting Jarvik's conclusions because, in the first place, it is only the snout region that has been studied in detail and examination of the entire anatomy might yield different results, and, in the second place, because the comparisons made were rather limited in scope. Of the Amphibia only *Salamandra* and *Rana* were discussed in detail, and, even more important, of the Rhipidistia only *Porolepis* and *Eusthenopteron* were available for study.

The present paper is concerned primarily with the evidence for a basic distinction between the "Porolepiformes" and the "Osteolepiformes," for all subsequent phylogenetic hypothesis must rest upon the validity of this proposed dichotomy.

For many Rhipidistia there is little material preserved in a fashion suitable for detailed palaeo-anatomical studies, but of the osteolepid genus *Ectosteorhachis* (previously confused with *Megalichthys*, see Thomson, 1964) from the Lower Permian of North America, much well preserved material exists. I have used this material to prepare a detailed account of the snout anatomy of *Ectosteorhachis*. The knowledge gained from this study, together with other information concerning different genera of Rhipidistia (Ørvig, 1957; Vorobjeva, 1959, 1960a, 1960b; Kulczycki, 1960; Thomson, 1962; Jarvik, 1962) which has become available since the date of Jarvik's original work, enables us to view the anatomy of the Rhipidistia from a broad and more truly comparative basis. The last section of this paper is a critical re-evaluation of Jarvik's theory in the light of this comparative study. Since the basis for Jarvik's theory was evidence from the nasal/ethmoid anatomy of the Rhipidistia, the present investigation is naturally centered in this region.

This study forms part of the work presented to the Department of Biology at Harvard University in fulfillment of the

requirements for the degree of Doctor of Philosophy. During my studies I have been greatly helped and encouraged at all times by my advisor, Professor A. S. Romer, and I must thank him also for the use of the collections and facilities of the Museum of Comparative Zoology. The staffs of the Palaeontology Preparation Laboratory and the Library at the Museum of Comparative Zoology have helped me with many kindnesses and courtesies. This study was undertaken while I was a recipient of North Atlantic Treaty Organization Science Studentship 3/60/955 administered by H. M. Department of Scientific and Industrial Research, London, during the years 1960 to 1963, and the Jeffries Wyman Scholarship at Harvard University during 1960/1961.

MATERIALS AND METHODS

The material of *Ectosteorhachis* used in this study comes from the collection of the Museum of Comparative Zoology at Harvard University. It has been collected in the Lower Permian "red-beds" of North Central Texas; several specimens of this collection were used in a previous study of *Ectosteorhachis* ("*Megalichthys*") made by Romer (1937).

The major part of the study has been made from a particularly complete skull (MCZ 8662) from the Belle Plains Formation, Wichita Group, Archer County, Texas, that was sectioned transversely at one-quarter millimetre intervals by the celloidin peel method. Experiments were made to stain the sections: a saturated solution of Alizarin Red S in 95 per cent ethyl alcohol used after the section had been oxidised by immersion in 0.25 per cent potassium permanganate gave the best results, but in general it was found that direct examination of the unstained section under a microscope was the best method of studying the sections. Wax-plate reconstructions were made of the snout region.

I have also used the series of sections made in the horizontal and sagittal planes previously prepared by Dr. Romer (cf. Romer, 1937).

Of other Osteolepidae, and of the Rhizodontidae, Porolepidae and the Holoptychidae, I have studied the collections of the Museum of Comparative Zoology at Harvard University, the American Museum of Natural History, the Chicago Natural History Museum, the British Museum (Natural History) and the Royal Swedish Natural History Museum.

ECTOSTEORHACHIS

Skeleton of the Snout Region

Dermal bones of the skull roof and palate. A full description of the dermal bones of the ethmoid region of the skull of *Ectosteorhachis* has already been given (Thomson, 1964). As shown in Figure 3, the dermal skull roof consists, in the ethmoid region, of a pair of parietal bones which bear the supraorbital lateral line canals forwards and mesially from the dermosphenotics; a single median postrostral bone; paired anterior postrostral bones; a compound naso-rostro-premaxilla (termed "premaxilla" throughout this paper); a lachrymal bone; prenarial and postnarial bones; and a series of four separate nasal bones which bear the supraorbital lateral lines, on each side, from the parietals forward to the ethmoid commissure with the infraorbital lateral line. The infraorbital lateral line canal, on each side, runs in a shallow loop, ventral to the naris and the pre- and postnarial bones, in its passage between the lachrymal and the premaxilla.

On the palate the vomers are roughly triangular in shape (Fig. 4) and the tooth-bearing ridge of the parasphenoid ends anteriorly at the level of the postnasal wall. The vomers form the posterior margin of an "anterior palatal recess" — a shallow recess formed between the anterior margin of the ethmoid endocranium and the premaxillae. The expanded bases of a pair of premaxillary "tusks," in the midline, separate the recess into two parts. The functional significance of the anterior palatal recesses will be discussed later.

External features of the endocranium. The endocranium of *Ectosteorhachis* has already been described in some detail by Romer (1937, pp. 18-22). My purpose here is therefore to add to Romer's account those details of structure not shown in his material, which was incomplete in the nasal region.

Figures 1 and 2 show the overall configuration of the endocranium. The nasal capsules of *Ectosteorhachis* are complete dorsally and laterally except for the foramina for the exit of various canals for nerves from the nasal cavity (e.g. Fig. 1, *f.ap.*). The anterior wall and the posterior wall of the capsule are pierced by canals for various nerves and vessels (discussed in the next section); the lateral wall is broken only by the fenestra endonarina. The median wall of the capsule is formed by the solid internasal wall; this is pierced by the canals carrying the olfactory tract and also by several vascular and nervous pathways.

The roof and very thin side walls of the nasal capsule are, for the most part, fused with the overlying dermal bones. On the medial face of the lateral wall of the capsule, immediately posterior to the fenestra endonarina, there is a small elliptically-shaped ridge of endocranial bone projecting into the nasal cavity. This ridge, which I have termed the crista lateralis (Figs. 5, 9, *c.l.*), bears on its median face a groove (Figs. 5, 9, *gr.c.l.*) which, from its relation to the external narial aperture, may have partially enclosed the tube for the external naris.

The posterior wall of the capsule, in addition to being pierced by the canals which in all probability carried the ophthalmicus superficialis seventh and profundus fifth nerves mentioned by Romer (1937), has a large opening in the ventrolateral corner (Figs. 3, 4, 5, 10 D and E, *p.v.f.*) — the posteroventral fenestra — the significance of which is rather enigmatical. Jarvik considered a similar fenestra in *Eusthenopteron* to represent a

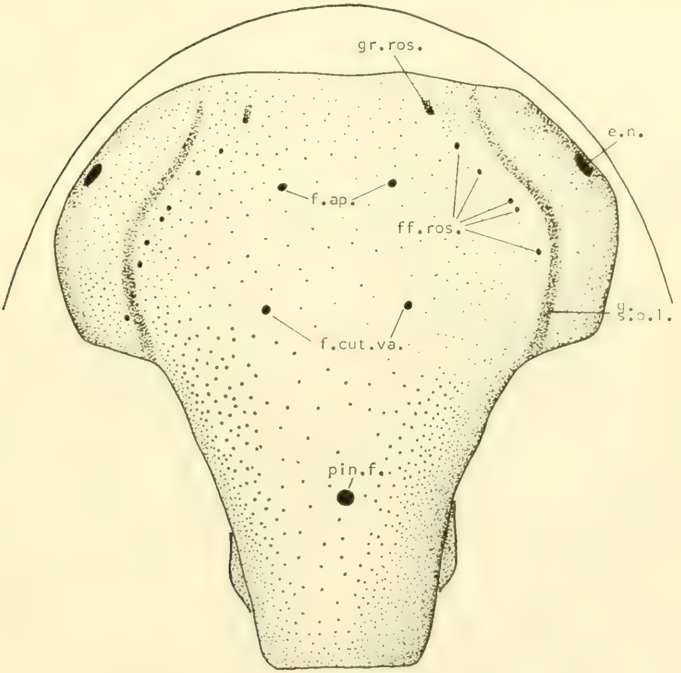


Figure 1. *Ectosteorhachis.* Ethmoid endocranium in dorsal view.

modified posterior external naris which might possibly be connected by means of a duct (the forerunner of the tetrapod nasolachrymal duct) with the orbital opening. It is not impossible that this fenestra served to permit the passage to and from the nasal cavity of large blood vessels.

The ventral wall of the nasal capsule is not preserved in any of the material studied by Dr. Romer or myself. In view of the otherwise excellent preservation of the specimens it seems most likely that the solum nasi was not ossified but was present in the living animal only in a cartilaginous form. The position of the choana may easily be inferred from the relative positions of the vomer, palato-quadrate and the dermal bones of the cheek.

The pars autopalatina of the palato-quadrate was inserted into the notch formed between the median part of the postnasal wall and the endocranium (Fig. 2, *n. pq.*). This notch is not lined with periosteal bone like the rest of the nasal region and it is possible that the junction between the endocranium and the palato-quadrate in this region was not a free articulation.

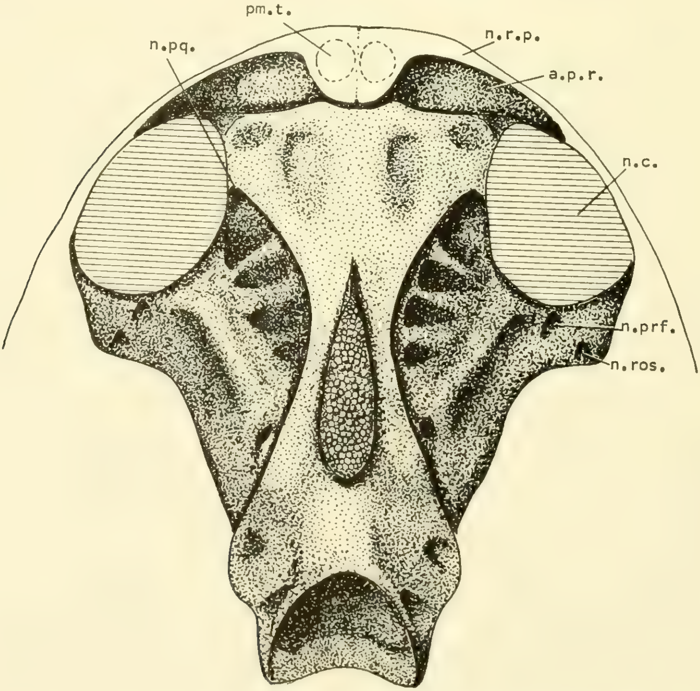


Figure 2. *Ectosteorhachis.* Ethmoid endocranium in ventral view.

The endocranial and associated cavities. In Figures 3 and 4, which show the general configuration of the endocranial cavities, the details of the hypophysial region have been restored, without modification, after the account of Romer (1937, figs. 9, 10).

The cranial cavity in the ethmoid division of the skull of *Ectosteorhachis* consists of spaces containing the hypophysial and pineal regions and the olfactory tracts. Since there is no part of the forebrain corresponding to the olfactory bulbs, it is assumed that the olfactory bulbs are represented by swellings in the canals for the olfactory tracts, as is the case in the Dipnoi (cf. Pinkus, 1895). There is no continuation of the cranial cavity anterior to the point of separation of the two olfactory tracts; the internasal wall contains no large cavities.

Immediately anterior to the level of the separation of the olfactory tracts there arises, from the ventral surface of the canal for each tract, a set of fine canals (Fig. 4, *cc.mea.*, *c.ana.*) that I have interpreted, judging from their position and distribution, as having carried vessels probably connected with the internal carotid artery. There are two sets of canals. A series of smaller ramifying canals pass forwards medial and ventral to the olfactory tract canal and terminate in the highly cancellous internasal wall (Fig. 4, *cc. mea.*). A single larger canal immediately separates from the smaller canals and runs forwards (Fig. 4, *c.ana.*) ventral to the olfactory tract canal; at a point just posterior to the nasal cavity it recombines with this canal.

Another set of canals arises from the dorsal surface of the canal for the olfactory tract just posterior to the nasal capsule; these canals (Fig. 3, *c.m.cut.va.*, *c.l.cut.va.*) seem also to have contained vascular elements and extend in three directions in the endocranium. (1) An anterior canal has a short connection back to the canal for the olfactory tract and a stout branch curving forwards over the nasal sac. It has a short cross-connection to the canal for the ophthalmicus superficialis seventh nerve (see below), as it passes through and above the postnasal wall. According to Romer (1937) there is a complete fusion of the two canals here and they enter the nasal cavity together. My material indicates, however, that the canals are distinct from each other and from the nasal cavity. The anterior canal disappears in the anterior part of the endocranium medial to the nasal capsule. (2) A median canal (Fig. 3, *c.m.cut.va.*) passes anteromedially and opens onto the dorsal surface of the endocranium below the median postrostral bone of the dermal skull roof (Fig. 3, *m.pr.*). (3) A lateral canal terminates in the lateral part of the endocranium behind the nasal cavity (Fig. 3, *c.l.cut.va.*).

Romer (1937, p. 32) has already noted that the posterior wall of the nasal capsule is pierced by two canals which seem to have carried the ophthalmicus superficialis VII and profundus V cranial nerves, the canal for the former lying dorsolateral of the canal for the latter. The canal for the profundus V (Fig. 3, *c.pr.V*) is a short simple tube through the postnasal wall; there is a slight connection within the postnasal wall with the canal for the ophthalmicus superficialis VII. The latter canal is entirely separate from the nasal cavity, within the postnasal wall. In addition to the connection with the canal for the profundus V and the anterior vascular canal noted above, there is given off from the canal for the ophthalmicus superficialis VII the first of

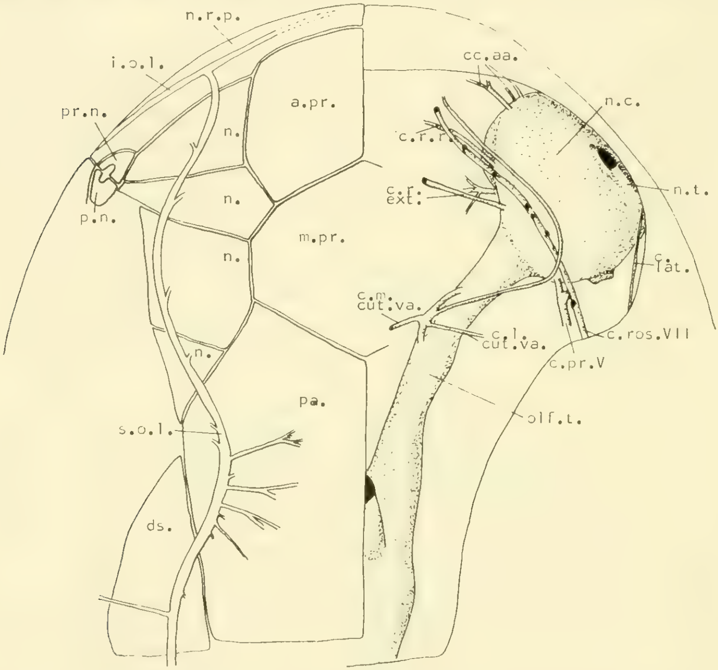


Figure 3. *Ectosteorhachis.* Endocranial cavities and the dermal bones of the skull roof. Dorsal view.

a series of dorsal branches which pass out of the endocranium (Fig. 1, *ff.ros.*) and obviously contained branches of the nerve supplying the sense organs of the supraorbital lateral line canal. The canal for the ophthalmicus superficialis VII curves forwards through the roof of the nasal capsule and emerges from the endocranium at about the level of the anterior nasal wall and thence continues in the space between the endocranium and the dermal bones.

The anterior wall of the nasal capsule is pierced by a series of fine canals (Figs. 3, 4, *cc.aa.*) which communicate with the palatal recess and the medial surface of the premaxilla.

A fine canal (Fig. 3, *c.lat.*) passes through the posterolateral corner of the nasal capsule from the medial surface of the lachrymal bone without entering the nasal cavity.

The medial wall of the capsule is pierced by two nerve canals in addition to the canal for the olfactory tract. The more posterior of the two canals (Fig. 3, *c.r.ext.*) leaves the nasal cavity

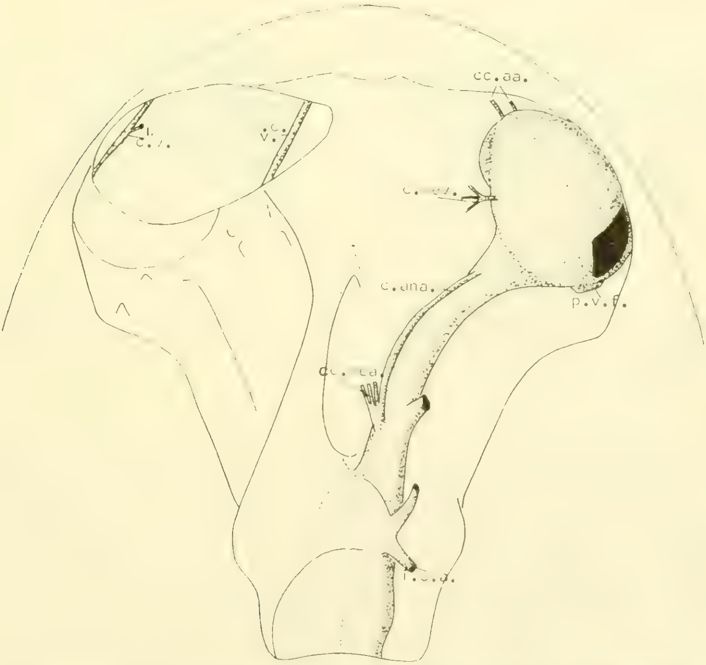


Figure 4. *Ectosteorhachis*. Endocranial cavities and dermal bones of palate. Ventral view.

just anterior to the canal for the olfactory tract and passes dorsally, anteriorly and medially to open at the foramen apicale on the dorsal surface of the endocranium (Fig. 1, *f.ap.*). Romer considered that the foramen apicale was the opening of the canal for the ophthalmicus superficialis VII, but the situation of this canal seems to indicate that it contained the ramus exterior of the profundus V nerve (discussion below). The more anterior canal piercing the medial nasal wall leaves the nasal cavity at the dorsal part of the anteromedial recess (discussed below). This canal (Fig. 3, *c.r.r.*) passes anteriorly to emerge on the anterior margin of the endocranium dorsal to the anterior palatal recess; it seems to have carried an anterior branch of the profundus V system.

Also opening through the medial wall of the capsule is a set of branching canals (Fig. 4, *c.mev.*) which ramify within the internasal septum. This canal system probably contained a set of veins draining into the nasal cavity.

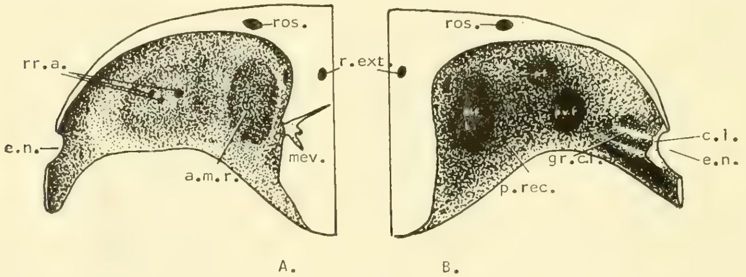


Figure 5. *Ectosteorhachis.* Nasal cavity. A. Left cavity in anterior view. B. Left cavity in posterior view. Graphical reconstructions from the sectioned specimen.

The nasal cavity itself is roughly elliptical in shape with the long axis of the ellipse lying at an angle of about 45° to the anteroposterior axis of the head. The inner surface of the nasal capsule is not ornamented and the only modifications of the otherwise smooth contour of its surface are caused by the posterior median recess (Fig. 5, *p.rec.*) into which the olfactory tract entered, and an anterior median recess (Fig. 5, *a.m.r.*) (termed the ventromedial recess by Romer, and already discussed by that author). The crista lateralis broadly separates a choanal recess from the rest of the nasal chamber. The groove on the median surface of the crista lateralis may have borne a short narial tube connecting the naris and the nasal chamber (Fig. 3, *n.t.*).

Certain of the dermal bones contain cavities which are clearly related to the canals for nerves and vessels which pass through the endocranium.

Each vomer is pierced by a medial and a lateral canal (Fig. 4, *m.c.v.*, *l.c.v.*) which are occasionally branched. There are no cross-connections between the canals, but the lateral canal, on one side of the specimen sectioned, has a dorsal branch which emerges on the dorsal face of the vomer underneath the nasal cavity. Since the solum nasi is not preserved it is not possible to detect whether or not this branch actually connected with the nasal cavity.

Neither vomerine canal can be traced posteriorly; it is assumed that the medial canal would have been continued medial to the palato-quadrate complex, between it and the parasphenoid bone, and it probably contained the palatine ramus of the seventh cranial nerve. The lateral canal must have been continued backwards lateral to the choana and between the palato-quadrate and the lachrymal; this canal probably contained the maxillary ramus of the fifth cranial nerve.

The nasal, parietal, premaxillary and lachrymal bones of the skull roof enclose a large canal (Fig. 8, *c.l.l.*) which, from its pathway over the skull roof, its relation to the course of the canal for the ophthalmicus superficialis VII nerve, and the disposition of its fine branches relative to the centres and modes of radiation of the dermal bones, obviously contained the supraorbital and infraorbital divisions of the lateral line system. The canal for the infraorbital lateral line, as it passes through the premaxillae and lachrymal bones, is surrounded by several smaller canals which branch and ramify with the lateral line canal and with each other. These smaller canals must surely have carried vessels and nerves associated with the lateral line organs, including, in all probability, the buccalis lateralis branch of the seventh cranial nerve. The only connections between the canal for the infraorbital lateral line and the medial surface of the dermal bones occur once in the lachrymal bone and once in the premaxilla.

The Nerves of the Ethmoid Region[1]

The fifth cranial nerve. The ramus profundus of the fifth cranial nerve leaves the cranial cavity through the space between the two divisions of the endocranium (see Romer, 1937). Of the further anterior course of the nerve nothing may be seen until it re-enters the endocranium through the postnasal wall (Fig. 3, *c.pr.V*). Within the nasal cavity the nerve probably divided into two main branches, a ramus medialis narium and a ramus lateralis narium (Fig. 6, *r.m.n., r. ln.*), as is the case in the Dipnoi and Amphibia. However, while the presence of a branching ramus medialis narium is shown by various canals through

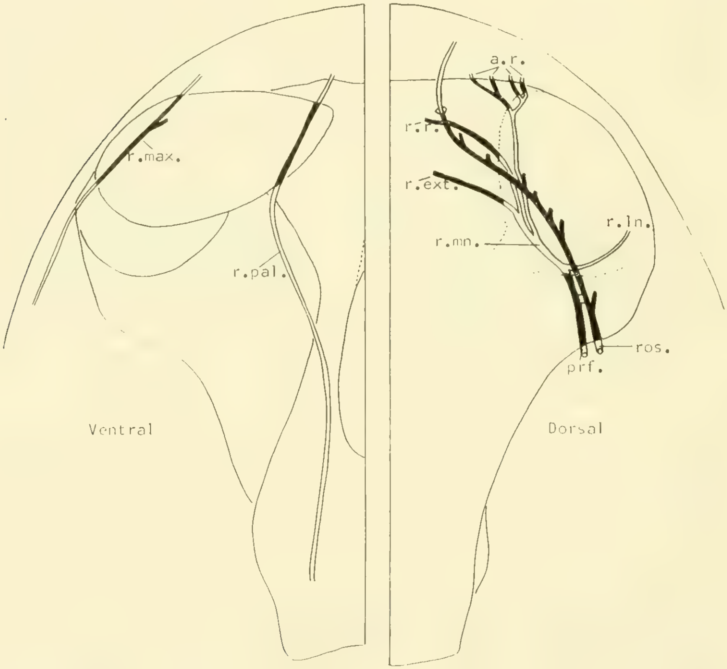


Figure 6. *Ectosteorhachis.* Reconstruction of the nervous system of the snout. Left in ventral view. Right in dorsal view. Portions of nerve course represented by an endocranial canal drawn in solid black, reconstruction in white.

---

[1] Unless otherwise stated, the terminology used in this section follows the system used by Jarvik (1942).

the medial wall of the nasal capsule, similar direct evidence of the path of the ramus lateralis narium is lacking.

The canal which opens out of the nasal cavity just anterior to the opening for the olfactory tract (Fig. 3, *c.r.ext.*) probably contained the "ramus exterior" of the profundus V; this nerve passed dorsally and medially to leave the endocranium at the foramen apicale. Anterior to this a second branch of the profundus V leaves the nasal cavity through the canal opening into the anterior palatal recess (Fig. 3, *c.r.r.*). I have termed this branch the "ramus rostralis" of the ramus medialis narium (Fig. 6, *r.r.*). The canal carrying this nerve has a slight connection with that carrying the ophthalmicus superficialis VII nerve, but anastomosis between these two nerves in this position seems unlikely and the connecting canal probably contained a small vessel. A third set of branches of the ramus medialis narium, which I have termed the "anterior rami" (Fig. 6, *a.r.*), pass through the anterior nasal wall.

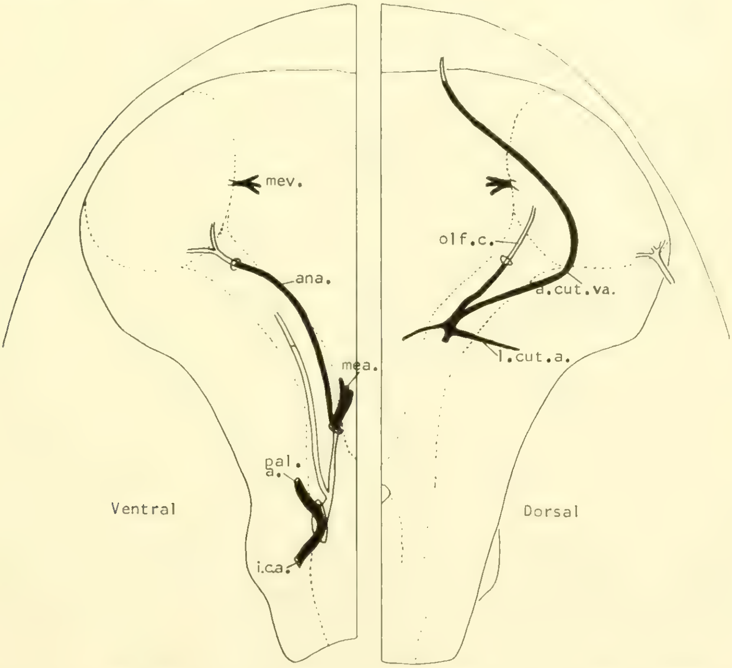


Figure 7. *Ectosteorhachis.* Reconstruction of vascular system. Left in ventral view, right in dorsal view. Portions of vascular system represented by endocranial canals drawn in solid black, reconstruction in white.

The ramus maxillaris of the fifth cranial nerve seems most likely to have been contained in the canal passing through the lateral edge of the vomer (Figs. 4, 8, *l.c.v.*). This nerve (Fig. 6, *r. max.*) thus corresponds to the "r.vot." of Jarvik (1942, fig. 61) and the branch of the maxillary fifth which in *Eusthenopteron* may have formed a post-choanal anastomosis with the ramus palatinus VII. Whether such an anastomosis existed in *Ectosteorhachis* can only be a matter for conjecture.

Other branches of the ramus maxillaris must have passed to and probably within the dermal bones of the anterior part of the cheek. If there was a ramus infraorbitalis it must have entered the nasal cavity at the problematical posteroventral fenestra or have passed forward entirely outside of the nasal cavity.

The seventh cranial nerve. The ramus ophthalmicus superficialis of the seventh nerve enters the endocranium through the canal, in the dorsal part of the postnasal wall, described above (Fig. 3, *c.ros.*VII). As it passes through the endocranium in a curved path corresponding to, but slightly medial to, the path of the supraorbital lateral line canal, the ramus ophthalmicus superficialis gives off a series of fine dorsal branches supplying the lateral line organs. Anteriorly, after emerging onto the surface of the endocranium, the nerve passes forwards and then laterally, curving around to the ethmoid commissure of the lateral line system; however, in this region of the snout it is extremely difficult to trace the finer details of the various nerve pathways.

The ramus palatinus VII seems to have been carried in a canal in the medial part of the vomer (Figs. 4, 8, *m.c.v.*). Anterior to the vomer the nerve probably passed into the anterior palatal recess region; posterior to the vomer it probably passed between the palato-quadrate and parasphenoid bones (Fig. 6, *r.pal.*).

Since the infraorbital lateral line is well developed in *Ectosteorhachis*, the ramus buccalis lateralis VII must also have been present. The path of the infraorbital lateral line in the nasal region (see Thomson, 1964) curves ventrally below the circumnarial bones, and thus in this region the lateral line canal is morphologically ventral to the level of the solum nasi. This being the case, it is unlikely that the ramus buccalis lateralis would have passed within the nasal cavity as it does in the genus *Eusthenopteron* (Jarvik, 1942); furthermore, only in two places, one within the lachrymal bone and one at the very tip of the premaxilla, is there any connection between the canal for the infraorbital lateral line and the medial face of the bones containing it. (Conceivably the anterior of these two connections served to pass branches of the ophthalmicus superficialis VII to the infraorbital part of the ethmoid commissure.) We have noted above that the canal for the lateral line is, in this region, surrounded by a set of smaller anastomosing canals also contained in the body of the dermal bones, and we must conclude that the ramus buccalis was most likely to have been carried in one of these canals.

The Vascular System of the Ethmoid Region

Arterial system. Romer (1937) has already described the arrangement of the internal carotid, palatine, and ophthalmic arteries in the hypophysial region of *Ectosteorhachis;* the further anterior courses of the palatine and ophthalmic arteries cannot be traced in the fossils.

After it has entered the cranial cavity the internal carotid can only be traced by the paths of those of its branches which subsequently leave the cranial cavity. The canals for such branches have been described above. A prominent set of branches (Fig. 4, *cc. mea., c.ana.*) appears to have passed out from the ventral surface of the canal for the olfactory tract just anterior to the separation of the two tracts. A set of three or four median ethmoid arteries (Fig. 7, *mea.*) ramify through the median part of the ethmoid endocranium. They pass right up to the tip of the endocranium, but their most anterior passage is very difficult to follow, since the endocranial bone in this region is extremely cancellous; accordingly I have restored them (Fig. 7) only in a diagrammatic fashion. A single and rather larger canal branching from the endocranial cavity at the same point (Fig. 4, *c.ana.*) also seems to have contained an artery, which I have termed the anterior nasal artery. This artery passes forwards beneath the olfactory tract right up to the nasal region where its canal rejoins that for the olfactory tract and presumably the artery enters the nasal cavity thereby.

The set of canals which branch off from the canal for the olfactory tract dorsally, just posterior to the nasal region, seem most likely to have contained arterial vessels also. I have termed these the cutaneous arteries; there are three main elements, anterior, median and lateral. The anterior cutaneous artery passes forwards dorsal to the olfactory tract and curves over the nasal region, following approximately the path of the supraorbital lateral line canal (Fig. 7, *a.cut.va.*). Immediately after the separation of this artery from the canal for the olfactory tract there is a short connection back to this canal (Fig. 7, *olf.c.*) which may have held a vessel. The series of short connecting canals between the canals for the anterior cutaneous artery, the ramus ophthalmicus superficialis VII and the profundus V may also have carried branches of this anterior artery. The median cutaneous artery passes anteromedially towards its fellow of the opposite side (in my material the canals did not appear to meet as Romer, 1937, had described), and terminates under the posterior part of the median postrostral bone. The lateral cutaneous artery terminates in the lateral endocranium posterior to the nasal capsule.

Venous system. There are fewer canals for the passage of veins in the ethmoid region than for arteries.

A set of branching canals opening into the anterior part of the posterior median recess of the nasal cavity (Fig. 4, *c.mev.*) seems to have contained a set of venous vessels draining the internasal part of the ethmoid endocranium. The finer branches of these ''median ethmoid veins'' which are not shown in the restoration (Fig. 7) seem to terminate in the same general region as do those of the median ethmoid arteries.

The wall of the posterolateral corner of the nasal capsule is pierced by a canal which may also have contained a small vein, the lateral nasal vein. This does not enter the nasal cavity (Fig. 3, *c.lat.*), but passes from the space between the dermal bones of the skull roof to the orbital cavity.

Since the arterial supply to the nasal cavity seems to have been well developed, there must have been a substantial venous system draining the nasal chamber. This is borne out by the fact that the veins draining the internasal wall also pass into the nasal chamber. There are two alternative routes by which veins may have left the nasal cavity: either they passed alongside the profundus nerve in its canal through the postnasal wall, or they passed through the posteroventral fenestra. There is no way of deciding between these alternatives. It may, however, be noted that the posterior opening of the canal for the presumed lateral nasal vein is in the same general region as the posteroventral fenestra, and in the absence of some other acceptable explanation of the function of the posteroventral fenestra, the possibility that it served for the passage of vascular elements should not be ignored.

As a final note on the vascular system it should be noted that the canals piercing the anterior wall of the nasal capsule may have contained vessels as well as nerves.

DISCUSSION

The Ethmoid Endocranium

The ethmoid endocranium has been described in the following rhipidistian genera: *Ectosteorhachis* (Romer, 1937, 1941); *Eusthenopteron* (Bryant, 1919; Stensiö, 1922; Holmgren and Stensiö, 1936; Sternberg, 1941; Jarvik, 1937, 1942, 1954); *Glyptolepis* (Jarvik, 1962); *Panderichthys* (Vorobjeva, 1960a); *Platycephalichthys* (Vorobjeva, 1959); *Porolepis* (Jarvik, 1942; Kulczycki, 1960); *Rhizodopsis* (Watson and Day, 1916; Säve-Söderbergh, 1936).

More brief accounts of these and other genera are also to be found in the literature.

Romer (1937) compared the endocranium of *Ectosteorhachis* with that of those forms then known. To this comparison further points may be added, as below.

Anterior palatal recesses.[1] In both *Ectosteorhachis* and *Megalichthys* the anterior palatal recess is divided into two parts by posterior expansions of the premaxillae in the midline. In *Megalichthys* (Thomson, 1964), division is aided by a "buttress" from the anterior part of the endocranium which fits up against the expansions of the premaxillae. In *Panderichthys* (also an osteolepid, see Thomson, 1962), the buttress of the endocranium is present but not the premaxillary expansion (see Vorobjeva, 1960a, fig. 1). In the rhizodontid *Eusthenopteron* the anterior palatal recess is undivided. In *Porolepis* (Porolepidae) and *Holoptychius* (Holoptychidae) the anterior palatal recesses are paired and entirely separate from each other. Each recess consists of a cavum prenasale which corresponds to the anterior recess in Osteolepidae and Rhizodontidae, and a cavum internasale which extends as a shallow depression under the ventral surface of the endocranium (Jarvik, 1942). The two cava internasalia are separated by the anterior part of the parasphenoid; the cava prenasalia are separated by a ridge of the endocranium which may correspond to the "buttress" found in some Osteolepidae.

---

[1] Also described by the terms "apical pits," "anterior palatal fenestrae."

Jarvik (1942) considered that these anterior palatal recesses in Rhipidistia contained glandular structures homologous with the various intermaxillary glands found in Recent Amphibia. It had already been suggested, however, that these recesses served for the reception of large "tusks" of the lower jaws when the jaws were occluded (Holmgren and Stensiö, 1936; Romer, 1937). Recent work by Kulczycki (1960), Thomson (1962), and Jarvik (1962) has confirmed this view. The characteristic shape of the recesses in the Porolepidae and Holoptychidae reflects merely the nature of the teeth at the tips of the lower jaws which, in these families (Ørvig, 1957; Jarvik, 1962), take the form of a pair of tooth whorls.

Pars ethmoidalis cranialis. Jarvik (1942) stated that in *Porolepis* and typically only in the Porolepidae and Holoptychidae, the cranial cavity in the ethmoid endocranium is continued anteriorly, beyond the point of separation of the canals for the two olfactory tracts, as a large space — the "pars ethmoidalis cranialis." This feature, he stated, was not present in the Osteolepidae or Rhizodontidae.

The inference in Jarvik's work (cf. Jarvik, 1942, fig. 45 A) is that the pars ethmoidalis cranialis contained the hemispheres of the forebrain which were situated anterior to the point of origin of the olfactory tracts. Jarvik thus supposed that the brain of *Porolepis* corresponded in its morphology to that of an urodele such as *Salamandra* (cf. Francis, 1934, pl. 9, figs. 51, 52), as opposed to that of other tetrapods and of *Eusthenopteron* which lack the pars ethmoidalis cranialis and in which the olfactory tracts are given off from the very anterior tip of the forebrain.

A review of the evidence, however, shows that the pars ethmoidalis cranialis does not occur in any consistent manner in the Rhipidistia. Kulczycki (1960) reported that it was absent in the material of *Porolepis* he studied[1] and Vorobjeva (1960a) stated that this cavity was present both in the osteolepid genus *Panderichthys* and the rhizodontid genus *Platycephalichthys* (see Thomson, 1962). When one further bears in mind that the cavity in the endocranium does not necessarily reflect the exact configuration of the brain contained therein, we must conclude that it is far from certain that a structure as inconsistent as the pars ethmoidalis cranialis contained any part of the cerebral anatomy.

---

[1] Some of Kulczycki's conclusions must be treated with reservation, since his material consisted only of natural casts.

The nasal capsules and nasal cavity. The nasal capsule has been described in detail only in *Eusthenopteron* and *Porolepis* (Jarvik, 1942; cf. Kulczycki, 1960). Jarvik concluded from his studies that the nasal cavity in *Porolepis* was fundamentally different from that of *Eusthenopteron;* in the following discussion I have compared *Ectosteorhachis* with both of these genera to determine whether or not this distinction may be maintained in the light of a wider comparison.

The nasal capsule and nasal cavity in *Eusthenopteron* (Jarvik, 1942, pp. 464-467) have a complicated configuration. The medial wall of the capsule, as in *Ectosteorhachis,* bears two prominent recesses, an anterior one — termed by Jarvik the ventromedial recess — which is homologous with the anteromedial recess in *Ectosteorhachis,* and a posterior recess into which, as in *Ectosteorhachis,* the olfactory tract enters.

The prenasal wall bears two horizontal ridges which were considered by Jarvik (1942, p. 443) to divide the anterior part of the nasal chamber into various recesses. A lateral horizontal ridge runs from the middle of the prenasal wall onto the lateral nasal wall; a smaller and more medial ''crista intermedia'' runs to the anterior corner of the medial wall of the cavity. Neither of these ridges is represented in *Ectosteorhachis.*

The lateral wall of the nasal capsule of *Eusthenopteron* bears a thick ledge anterior and ventral to the external narial aperture and projecting as a flange into the nasal cavity. This large structure is termed by Jarvik the ''processus intermedius''; its anterior part connects with the lateral horizontal ridge of the prenasal wall. A process from the lateral rostral dermal bone projects onto the processus intermedius and into the nasal cavity as a slip of bone — the processus dermintermedius. These two processes do not have any direct equivalents in *Ectosteorhachis;* the possible homology of the processus intermedius with the crista lateralis of *Ectosteorhachis* is discussed below.

In *Porolepis* (Jarvik, 1942, pp. 367-372, esp. figs. 40, 42; Kulczycki 1960, pp. 74-75, 86-88, fig. 3) there are three main ridges on the inner surface of the nasal capsule, all on the lateral wall. Again, whether these ridges actually reflect any functional division of the nasal sac is uncertain. The most prominent ridge runs from the anterior external naris to the communal opening for the posterior external naris and the choana. It separates the narial openings from the choanal opening, and, being a quite high ridge, has been supposed by Jarvik (1942, p. 402) to have divided the lateral part of the nasal sac into two recesses, the more ventral of which he homologises with Jacobson's organ of urodeles. Jarvik terms this ridge, in accordance with the supposed relation with the Urodela, the crista rostro-caudalis. Kulczycki (1960), however, believes that the ventral recess so delimited is merely a chamber containing the choana and he terms the ridge "crista subnarina" to avoid hypothetical considerations of phylogeny.

The two other ridges on the lateral nasal wall of *Porolepis* are the crista orbito-rostralis which runs from the endochoanal notch to the anteroventral margin of the anterior external naris, and a thickening of the ventral rim of the fenestra endonarina anterior which Kulczycki, supposing it to be homologous with the similar structure in *Eusthenopteron*, terms the process intermedius.

The crista orbito-rostralis is not present as such in either *Ectosteorhachis* or *Eusthenopteron*, but it is interesting to reflect upon the question of the relationship of the crista subnarina (crista rostro-caudalis) of *Porolepis* to the crista lateralis of *Ectosteorhachis*. Both structures are situated anterior to the (anterior) external naris and pass backwards dorsally to the choana, separating the choanal recess from the main nasal chamber: they seem quite likely to be homologous structures.[1]

The crista lateralis is lacking in *Eusthenopteron*, but in this genus the processus intermedius (and dermintermedius) has taken over the function of separating the choana and external naris. We have already noted, above, a possible homologue of the processus intermedius in the thickening of the ventral margin of the anterior naris of *Porolepis*, and it is possible to set up the following scheme by which the various characteristic arrangements of the nasal cavity in *Porolepis*, *Eusthenopteron* and *Ectosteorhachis* may be related one to another.

It seems likely that the ancestral form linking the early porolepid fishes to the later Devonian Osteolepidae and Rhizodontidae was a primitive osteolepid with the external naris situated fairly far forward; there may even still have been two external nares, as has been reported for *Panderichthys* (Vorobjeva, 1960a). The ventral rim of the narial aperture(s) was probably enlarged as a thick ridge extending backwards to separate the naris from the choanal recess. This ridge would correspond to the crista subnarina (crista rostro-caudalis) of *Porolepis* and also to a process intermedius. In the Devonian Osteolepidae the more anterior part of the ridge was probably developed into a processus intermedius and this may even have been overlain by a processus dermintermedius from the lateral rostral bone. In the later Osteolepidae the more posterior part of the subnarinal ridge developed as the crista lateralis; this change is probably related to a migration of the narial aperture backwards. There is no dermal process comparable to the processus dermintermedius, and indeed, in *Ectosteorhachis*, the part of the lateral nasal wall bearing the crista lateralis is overlain by the postnarial bone (= tectal of *Osteolepis*, see Thomson, 1964) rather than by that part of the prenarial bone which corresponds to the lateral rostral bone.

---

[1] If Jarvik is correct in believing that the posteroventral fenestra of *Eusthenopteron* (and *Ectosteorhachis*) corresponds to the posterior external naris, the crista lateralis would have the same relations with the anterior naris, choana, and posterior naris as the crista subnarina in *Porolepis*.

The Rhizodontidae seem to have developed from the Osteolepidae. In the rhizodontids the naris has retained its relation to the lateral rostral bone, the processus intermedius is well developed, and the posterior part of the subnarinal ridge is lost. The processus dermintermedius is well developed and may extend onto the prenasal wall of the nasal capsule (Jarvik, 1942). We may conclude that the ethmoid region of the endocranium is apparently constructed according to a single general pattern in *Porolepis*, *Eusthenopteron* and *Ectosteorhachis*. Furthermore, the osteolepid *Ectosteorhachis* is observed to differ from the rhizodontid *Eusthenopteron* no less greatly than either of these genera differs from the porolepid *Porolepis*.

The Nervous System of the Snout

Details of the presumed course of the various nerves of the snout region of Rhipidistia have been given for the following genera only: *Porolepis* (Jarvik, 1942; Kulczycki,[1] 1960); *Eusthenopteron* (Jarvik, 1937, 1942); *Ectosteorhachis* (Romer, 1937). Details of the foramina for the profundus V and ophthalmicus superficialis VII nerves of *Osteolepis* and *Rhizodopsis* are given by Watson (1926) and Säve-Söderbergh (1936), respectively.

The fifth cranial nerve: ramus profundus. In *Ectosteorhachis*, *Megalichthys*, *Osteolepis*, *Rhizodopsis*, and most species and specimens of *Eusthenopteron*, the profundus V enters the nasal capsule by means of a single foramen in the postnasal wall. In *Porolepis*, according to Jarvik (1942), the profundus branches within the orbital region so that two or more rami enter the nasal capsule through separate foramina in the postnasal wall. According to Kulczycki (1960), the profundus in *Porolepis* branched within the postnasal wall itself; this is reported to be the case also in some specimens, at least, of *Eusthenodon* (*Eusthenopteron*) *wenjucovi* (Jarvik, 1937). It must be presumed that in all genera of Rhipidistia the profundus branched either inside or outside the nasal cavity to innervate both the mesial and lateral part of the nasal cavity, but that the actual site of the branching is somewhat variable.

---

[1] Only the better based of Kulczycki's conclusions are considered here.

There were most probably two main branches of the profundus within the nasal cavity — the ramus medialis narium and the ramus lateralis narium. In all cases the ramus medialis narium is the better developed, innervating, in addition to the nasal apparatus, the septum nasi and the anteromedial parts of the snout.

In *Eusthenopteron* and *Ectosteorhachis* the only branch of the profundus V to pass out through the dorsal surface of the endocranium is the ramus exterior. In *Porolepis*, according to Jarvik (1942), the profundus V leaves the nasal cavity through several fine canals which pierce the dorsal wall of the nasal capsule. One of the canals he described (1942, fig. 43, c.cut.va.) is homologous with the ramus exterior but, according to Kulczycki (1960), the remainder of these fine canals actually belong to the superficial ophthalmic branch of the seventh cranial nerve and do not arise from the profundus V which is very similar to that of other Rhipidistia.

We have seen that the ramus medialis narium in *Ectosteorhachis* has a number of medial and anterior branches and these are comparable to the branches of this nerve in *Eusthenopteron* (cf. Jarvik, 1942, fig. 61). In Jarvik's restoration (1942, p. 376) the ramus medialis narium of *Porolepis* left the nasal cavity only by means of the dorsal branches mentioned above, but Kulczycki's restoration (1960, fig. 5) includes one anteroventral canal opening into the anterior palatal recess of *Porolepis* which seems to correspond to the naso-basal canal (carrying a terminal branch of the ramus medialis narium through the prenasal wall) in *Eusthenopteron* and *Ectosteorhachis* (Jarvik, 1942, fig. 60, cvn-b; cf. this paper Fig. 3, *cc.aa.*).

As restored by Jarvik, the ramus lateralis narium in *Porolepis* has branches which leave the nasal capsule through the lateral nasal wall (Jarvik, 1942, fig. 42A, ec.pr.l.); comparable elements are lacking in *Eusthenopteron* and *Ectosteorhachis*. Jarvik also described in *Porolepis* a third branch of the profundus system which enters the ventrolateral part of the postnasal wall through the "orbitorostral passage" (1942, fig. 42 B, e.cr.). After passing along the ventral surface of the nasal sac this nerve leaves the nasal cavity at a foramen in the prenasal wall, but apparently does not pierce this wall. Kulczycki (1960) found no traces of the orbitorostral passage in his material of *Porolepis,* but he did find a blind canal leading from the nasal cavity into the prenasal wall; this canal, which Kulczycki terms the "para-apical canal," has, however, a different orientation from that

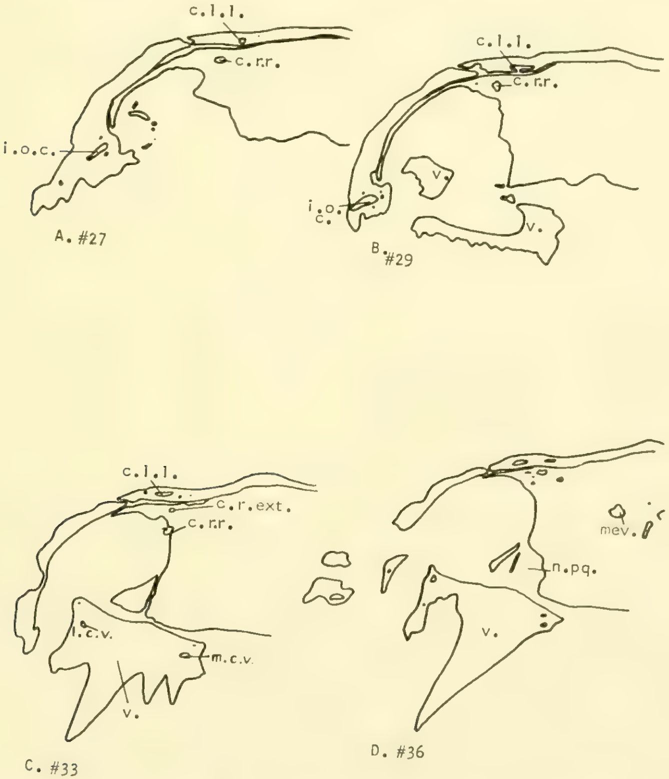


Figure 8. *Ectosteorhachis.* Right nasal cavity, anterior division. #27, at tip of snout; #29 showing anterior margin of vomer; #33 showing anterior margin of external naris; #36 through naris.

described by Jarvik, and in Kulczycki's opinion could only have contained a blood vessel.

We may conclude that the pattern of the ramus profundus V is essentially similar in all Rhipidistia.

Fifth cranial nerve: ramus maxillaris. Jarvik (1942) stated that in *Porolepis* this nerve did not reach as far anteriorly as the nasal region but terminated in the orbit. Kulczycki, however, claimed that there is evidence, in the form of a groove in the lateral nasal wall (Kulczycki, 1960, p. 92), that there was a truncus infraorbitalis extending into the nasal region.

In *Eusthenopteron,* Jarvik (1942, p. 477) traced certain branches of the ramus maxillaris but only part of his restoration is based upon the positive evidence of endocranial canals. What little I have been able to discover of the ramus maxillaris in *Ectosteorhachis* shows that it is generally similar to that of *Eusthenopteron,* but in most major respects our knowledge of this nerve in Rhipidistia is rather unsatisfactory.

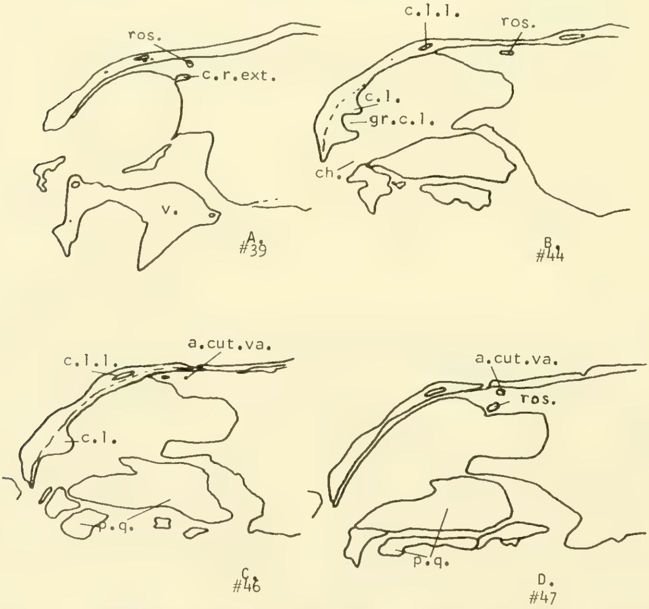


Figure 9. *Ectosteorhachis.* Right nasal cavity, median division. #39 through posterior part of external naris; #44 through crista lateralis; #46 and #47 showing beginning of entry of the olfactory tract canal into the posterior median recess.

The seventh cranial nerve: ramus ophthalmicus superficialis. In *Eusthenopteron* this ramus passes from the orbit through the postnasal wall and out onto the dorsal surface of the endocranium in a canal which has no connection with the lumen of the nasal cavity. In *Ectosteorhachis* the path of the nerve is exactly the same, although Romer (1937, fig. 8) mistakenly described the nerve as entering the nasal cavity. In both genera there may be, within the postnasal wall, a small canal connecting this nerve canal with that for the profundus V.

According to Jarvik's (1942) interpretation of the structure of *Porolepis*, the ramus ophthalmicus superficialis does not enter the nasal cavity, but Kulczycki (1960) presents evidence that the nerve does enter the cavity, either via a separate canal of its own or through that for the profundus V nerve, and that it passes along the dorsomedial part of the nasal cavity giving off branches through the endocranium to the supraorbital lateral line canal. These branches are the ones that Jarvik (see above) attributed to the profundus V nerve.

Seventh cranial nerve: ramus buccalis lateralis. Nothing is known concerning this nerve in *Porolepis*. Jarvik believed that it might have passed through the orbitorostral passage (the existence of which has been disputed by Kulczycki). The situation in *Eusthenopteron* is also vague although Jarvik (1942, pls. 11, 12 and 13) described a gap between the dermal bones and the nasal capsule in which such a nerve might have passed. *Ectosteorhachis* differs from *Eusthenopteron* in that the infraorbital lateral line canal is situated ventral to the level of the solum nasi, and the rather meagre evidence available indicates that the nerve may have been contained in the dermal bones of the anterior cheek region.

Seventh cranial nerve: ramus palatinus. This nerve seems to have occupied exactly the same position in *Porolepis, Eusthenopteron* and *Ectosteorhachis.*

Anastomoses in the nervous system. The two main groups of living Amphibia, Anura and Urodela, are characterized and may be distinguished by distinct patterns of anastomoses between the palatinus VII, maxillaris V and profundus V nerves (e.g. Coghill, 1902). Jarvik has attempted to show that the Rhipidistia of the families Porolepidae and Holoptychidae agree in this respect with the Urodela, and that the families Osteolepidae and Rhizodontidae agree with the Anura. A main point in Jarvik's thesis is the position of the anastomosis between the palatinus

VII and the maxillaris V nerves, behind the nasal capsule in the Anura and medial to the choana in the Urodela.

Unfortunately, the evidence concerning possible anastomoses in the Rhipidistia is rather incomplete, although Jarvik (1962) states that he has found new evidence in the anatomy of the porolepid *Glyptolepis* to confirm his original suggestions. My material

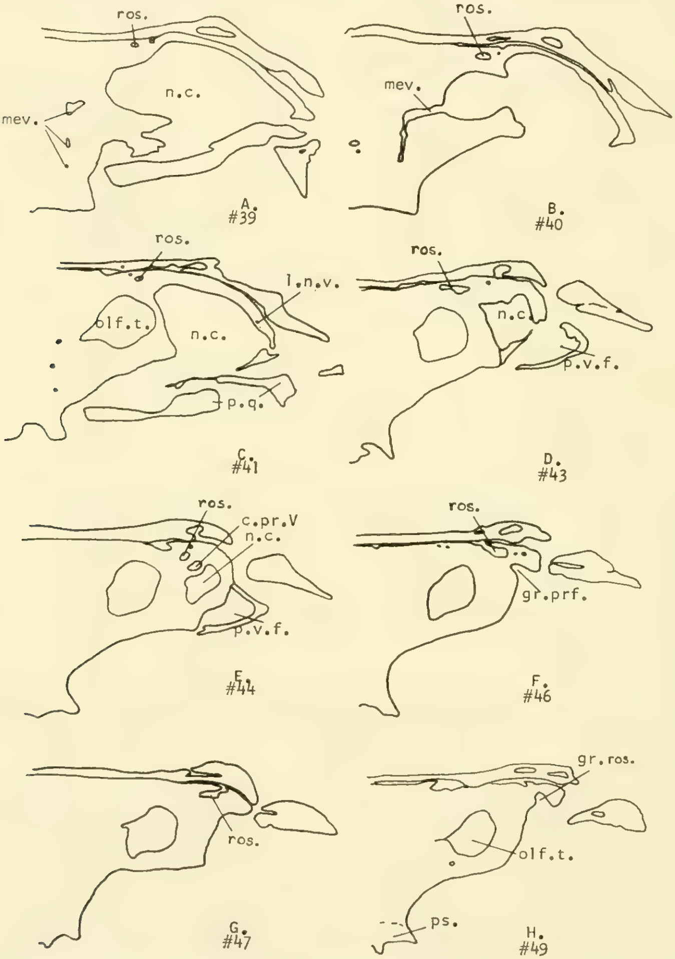

ros.
n.c.
mev.
A.
#39
ros.
mev.
B.
#40
ros.
l.n.v.
olf.t.
n.c.
p.q.
C.
#41
ros.
n.c.
p.v.f.
D.
#43
ros.
c.pr.V
n.c.
p.v.f.
E.
#44
ros.
gr.prf.
F.
#46
ros.
G.
#47
gr.ros.
olf.t.
ps.
H.
#49

Figure 10. *Ectosteorhachis.* Left nasal cavity. Series of sections through posterior part of the cavity, showing the postnasal wall and the associated nerve canals.

of *Ectosteorhachis* sheds little light on the problem; there is no indication of a connection between the palatinus VII and the maxillaris V as they pass through the vomer or in the space between the vomer and the palato-quadrate.

The canal for the ramus maxillaris V, as it passes through the vomer, gives off one, sometimes two, fine canals to the dorsal surface of the bone, but since the solum nasi is not preserved, I cannot tell whether they might represent evidence of an anastomosis with the branches of the profundus V in the nasal cavity. They may have carried small vessels.

Both the profundus and maxillary rami of the fifth cranial nerve of *Ectosteorhachis* have branches which, as in *Eusthenopteron*, terminate close together in the most dorsal part of the anterior palatal recesses. It is not possible to tell whether or not these nerve branches anastomosed here, although Jarvik states that this was the case.

In summary, we may conclude that in all major respects in which it is fully known, the pattern of the nervous system is essentially similar in *Ectosteorhachis*, *Eusthenopteron* and *Porolepis*.

The Vascular System of the Snout

No thorough review of the vascular system of the snout of Rhipidistia may be made, since the only genus in which it is even moderately well-known is *Ectosteorhachis*. Kulczycki (1960, fig. 5) attempted a reconstruction of the vascular system of *Porolepis*, but this must be treated with reservation. He did, however, find a trace of a canal which might have carried a vena cerebralis anterior — described elsewhere only in *Rhizodopsis*[1] (Säve-Söderbergh, 1936).

What little Jarvik was able to restore of the vascular system of *Eusthenopteron* (1942, p. 480) seems to agree fairly well with the arrangement in *Ectosteorhachis*.

CONCERNING A DIPHYLETIC ORIGIN OF THE TETRAPODS FROM WITHIN THE RHIPIDISTIA

Reference has been made throughout this work to the distinctions that Jarvik (1942) has drawn between the genera *Porolepis* and *Eusthenopteron* with respect to the detailed anatomy of the snout region. From his study of the snout anatomy of the Gnathostomata Jarvik drew the following conclusions:

---

[1] I have seen the specimen studied by Säve-Söderbergh, but since he used the "shatter technique" it is now impossible to learn anything further from the specimen.

1. That the four families of Rhipidistia may be considered to belong in two highly distinct groups: the ''Porolepiformes'' (comprising the families Porolepidae and Holoptychidae) and the ''Osteolepiformes'' (comprising the Osteolepidae and the Rhizodontidae).
2. That the two major groups of Recent Amphibia, Urodela and Anura, differ greatly from one another in their snout anatomy and must be considered to have arisen separately from different fish ancestors.
3. That the Urodela differ from the Anura in exactly the same characteristics as the ''Porolepiformes'' differ from the ''Osteolepiformes,'' and that the Urodela and Anura are direct descendants of the ''Porolepiformes'' and ''Osteolepiformes'' respectively.

The anatomical study of *Ectosteorhachis* set down above provides us with a body of new evidence concerning the anatomy of the ''Osteolepiformes'' which had previously been known only from study of *Eusthenopteron.* It is now possible to discuss proposition 1 (above) in considerable (comparative) detail. Discussions of the interrelationships of the Amphibia belong elsewhere than in this paper; Parsons and Williams (1962 and 1963), Eaton (1959), Schmalhausen (1959), Szarski (1962) and others have discussed the evidence for and against a fundamental separation of the Urodela and Anura. With respect to such discussion it should be noted that the ancestry of the Recent Amphibia is known only from very incomplete palaeontological evidence and discussion relies heavily on evidence from the anatomy of living forms. I shall confine myself to a consideration of the evidence, in the snout anatomy, for a separation of the Rhipidistia into ''porolepiforms'' and ''osteolepiforms'' with special regard to the phylogenetic implications of this proposed separation.

In his summary of supposed distinctions between the ''Porolepiformes'' and ''Osteolepiformes'' Jarvik (1942, p. 489, *et seq.*) enumerated some 26 points by which *Porolepis* (and thus the ''porolepiforms'') might be interpreted as differing from *Eusthenopteron* (and thus, typically, the ''osteolepiforms''). I propose now to examine each of these points in turn, in the light of the new evidence presented in the preceding pages.

Several of the 26 points overlap each other and we may group together first those dealing with the nature of the anterior palatal recesses and the general arrangement of the ethmoid endocranium.

1. "The internasal wall in *Eusthenopteron* is narrow and forms a solid nasal septum. The internasal wall in *Porolepis* is broad and lodges both the ethmoidal part of the cranial cavity and the paired cavum internasale" (1942, p. 489).[1]

2. "The divisio prenasalis communis is longer and narrower in *Eusthenopteron* than in *Porolepis*. On the lateral parts of its lower face in *Eusthenopteron* are a pair of shallow, ventrally open prenasal pits, situated far apart from each other; to these there is no equivalent in *Porolepis*. In *Porolepis*, on the other hand, the divisio prenasalis communis lodges the paired and comparatively deep cava prenasalia, which form the direct anterior continuation of the cava internasalia and are situated close to each other" (1942, p. 489).

3. "Point three" states that the "shallow paired" anterior palatal recesses in *Eusthenopteron* contained intermaxillary glands directly equivalent to those found in the anterior part of the palate in the Anura (p. 489, cf. p. 506) and that the cava internasalia of *Porolepis* contained intermaxillary glands arranged in the same manner as in Urodela (p. 489, cf. p. 400).

4. "The nasal cavities are fairly close to one another in *Eusthenopteron*, whereas they lie far apart in *Porolepis*" (p. 489).

26. "The anterior palatal fenestra in *Eusthenopteron* is comparatively small, lies entirely in front of the vomers underneath the divisio prenasalis communis, and does not form the ventral opening of any large cavity. The anterior palatal fenestra in *Porolepis* is large, lies chiefly between the vomers underneath the internasal wall, and in it are seen the ventral openings of the cava internasalia and prenasalia" (p. 493).

It should be noted that Jarvik distinguishes in his terminology between the apical pits and their "openings" the anterior palatal fenestrae; I prefer to use the term "anterior palatal recess" for the whole structure. Jarvik states that there are a pair of "prenasal" (equals "apical") pits in *Eusthenopteron;* but these are merely the two halves of an essentially undivided anterior palatal recess (cf. Jarvik, 1942, fig. 56). In *Ectosteorhachis* the anterior palatal recesses are definitely paired, and this is the case in *Megalichthys* and *Panderichthys*, as well as in *Porolepis* and *Holoptychius*. It has been noted above that the cava internasalia of "porolepiforms" and the anterior palatal recesses of "osteolepiforms" are homologous structures and that their characteristic nature reflects only the nature of the teeth at the tips of the lower jaw rami. Thus there is a difference in the shape of the recesses in the two groups, but, since no glandular structures are involved, comparisons with the Recent Amphibia are not justified.

---

[1] In this and the following quotations, abbreviations and references to figures in the original text have been omitted.

It has been noted also that the presence or absence of an ethmoid division of the cranial cavity — the pars ethmoidalis cranialis — is of random occurrence in the families of Rhipidistia and does not characterise any particular group.

As has been pointed out in a previous paper (Thomson, 1962), the internasal wall in the "osteolepiforms" may be broad or narrow and there is no evidence to support the theory that the presence or absence of the cava internasalia or the pars ethmoidalis cranialis is correlated simply with the relative width of the internasal wall or the relative size of the nasal sacs (cf. Schmalhausen, 1959; Romer, 1962; Szarski, 1962).

5. "The lamina nariochoanalis is in *Eusthenopteron* formed by the lateral nasal wall, in *Porolepis* both by the lateral nasal wall and an adjacent part of the solum nasi" (1942, p. 490).

The solum nasi is not preserved in *Ectosteorhachis*. But whereas in the postchoanal region the lateral nasal wall curves slightly underneath the nasal cavity (Fig. 9, A, B), in the choanal region this slight ledge is not present (Fig. 8, A, B), and this may indicate that the lamina nariochoanalis was formed only by the lateral nasal wall.

6. "*Eusthenopteron* has no equivalent to Seydel's palatal process in *Porolepis*" (p. 490).

Jarvik's identification of a small backwardly directed process on the anterolateral margin of the choanal aperture in the solum nasi of *Porolepis* as an homologue of the Seydel's palatal process of Urodela has been criticized by Kulczycki (1960) who has pointed out that if the subnarinal crest of *Porolepis* (see above) is homologised with the crista rostrolateralis of Urodela, then the small choanal process which lies "along its prolongation" is in a different position from that of Seydel's palatal process in urodeles. The process was not seen in *Ectosteorhachis*.

7. "The fenestra endonarina anterior and the fenestra endochoanalis are comparatively large in *Eusthenopteron*" (p. 490).

This does not seem a character of great phylogenetic importance. In *Ectosteorhachis* the fenestra endonarina is relatively slightly smaller than that of *Eusthenopteron;* the fenestra endochoanalis is of the same relative size.

8. "The fenestra endonarina posterior in *Eusthenopteron* is an opening in the postnasal wall leading backwards to the anterior ventro-lateral part of the orbit, and is separated ventrally by an endoskeletal bridge from the fenestra endochoanalis; in *Porolepis* it lies in the lateral nasal wall and is continuous ventrally with the fenestra endochoanalis" (p. 490).

The posteroventral fenestra of *Ectosteorhachis* corresponds to the opening in the postnasal wall of *Eusthenopteron* which Jarvik has homologised with the posterior external naris of *Porolepis.* It is difficult to tell whether Jarvik's proposed homology is justified or not; it seems to me that this fenestra may possibly have been one of the main openings through which the venous vessels left the nasal cavity and it is not impossible that nerve branches passed through it. Jarvik assumed that this fenestra connected by means of a duct (the forerunner of the nasolachrymal duct [1942, p. 537]) with the orbit but since the soft anatomy is not preserved there is no way of checking this hypothesis.

It is interesting to note that Vorobjeva (1960a) has described the osteolepid *Panderichthys* as having two external nares, the posterior of which is confluent with the endochoanal aperture. If this observation is substantiated this genus may thus represent some sort of link between the "Porolepiformes" and the "Osteolepiformes" with respect to this important character.

14. Point 14 refers again to the difference in the relative positions of the posterior external naris in *Porolepis* and its "homologue" in *Eusthenopteron,* and mentions again the possible homology of this structure in *Eusthenopteron* with the tetrapod nasolachrymal duct. This has been dealt with above.

9. "No canal corresponding to the nasobasal canal in *Eusthenopteron* exists in *Porolepis.* On the other hand the orbitorostral passage and the canal *c.vl* in *Porolepis* have no equivalents in *Eusthenopteron*" (p. 490).

The nasobasal canal carried the terminal branch of the ramus medialis narium of the profundus V nerve through the anterior nasal wall into the anterior palatal recess in *Eusthenopteron:* a similar canal is present in *Ectosteorhachis.* As mentioned above, Kulczycki (1960) has noted a canal in *Porolepis* also which may correspond to this canal.

The orbitorostral passage was not found in *Ectosteorhachis.* Kulczycki could not find this passage in his material of *Porolepis.*

The "canal *c.vl*" is something of an enigma; it lies in the lateral part of the postnasal wall of *Porolepis* and was supposed by Jarvik to carry a lateral branch of the profundus V nerve. However, it could very possibly have contained a blood vessel, particularly a vein, draining the nasal cavity. It is not present in *Ectosteorhachis.*

10. "In *Eusthenopteron* there is a single nerve-canal leading upwards from the nasal cavity to the dorsal face of the ethmoidal region; in *Porolepis* a great many nerve-canals ascend from the nasal cavity to the dorsal face of the ethmoidal region, piercing the dorsal part of the medial nasal wall, the adjacent part of the prenasal wall, and the medial parts of the tectum nasi" (p. 490).

Point 19 refers to the same subject: "The n. profundus in *Eusthenopteron* was comparatively weakly developed. . . . The n. profundus in *Porolepis* was strongly developed. . . . In the nasal cavity the medial nasal branch divided into numerous dorsal branches" (p. 491-492).

As has been noted in the previous discussion, the ramus profundus of the fifth cranial nerve seems to be developed in approximately the same manner in *Porolepis, Eusthenopteron* and *Ectosteorhachis.* The canals passing through the dorsal wall of the nasal capsule of *Porolepis* seem to pertain to the ophthalmicus superficialis VII nerve rather than to the profundus V. Thus, whereas the rami profundi of "Porolepiformes" and "Osteolepiformes" are similar, there may be a difference in the path of the ophthalmicus superficialis nerve — within the nasal cavity in *Porolepis*, and external to the nasal cavity in *Eusthenopteron* and *Ectosteorhachis.*

11. "The postnasal wall is pierced in *Eusthenopteron* by a single and not particularly wide profundus canal; in *Porolepis* by a wide medial and one or several narrower lateral profundus canals" (p. 490).

We have noted above that there may be some variation in the number of canals through which the profundus nerve enters the nasal cavity.

12, 13, 15. Points twelve and thirteen deal with the apparent subdivision of the chamber of the nasal capsule into recesses by the presence of various ridges and crests on the medial surfaces of the walls. Point 15 may also be discussed here, since it states that "The large differences in the nasal cavity show that there must have been considerable differences [between *Eusthenopteron* and *Porolepis*] in the development of the nasal sac" (pp. 490-491).

The subject of the ridges and crests of the nasal capsule has been reviewed above and we have seen that the conditions in *Porolepis*, *Eusthenopteron* and *Ectosteorhachis* may possibly be related to each other. The processus intermedius (or its homologue) may be present in *Porolepis* as well as in *Eusthenopteron* and the subnarinal ridge seems to be present, slightly modified, in all three genera.

It is not possible to decide with any degree of certainty whether or not the apparent morphological subdivisions of the nasal capsule represent any functional anatomical features of the nasal sac. For example, the ventromedial recess of *Eusthenopteron* corresponds exactly to that of *Ectosteorhachis*, but whether this recess of the nasal cavity contained a diverticulum of the nasal sac, and whether such a diverticulum, if present, would have contained Jacobson's organ (cf. Jarvik, 1942, pp. 483, 536) cannot be decided from the fossils alone. And while answers to such questions may be formulated from comparisons with the Recent Amphibia, the objective purpose of the study would then be defeated.

16. "The forebrain in *Eusthenopteron* was of approximately the same breadth as the diencephalon; . . . The bulbi olfactorii in *Eusthenopteron* lay close to one another immediately in front of the hemispheres, whereas in *Porolepis* they were situated far apart at the lateral sides of the hemispheres" (p. 491).

This apparent distinction arises from interpretation of the pars ethmoidalis cranialis of *Porolepis* as having contained the "hemispheres of the forebrain." In fact, available evidence now indicates that the pars ethmoidalis cranialis, which is of random occurrence throughout the Rhipidistia, did not contain any part of the brain anatomy, and that the brain of *Porolepis* was probably not greatly different in overall configuration from that of *Eusthenopteron*.

17. "The lateral parts of the snout were in *Eusthenopteron* supplied mainly by the r. maxillaris V, in *Porolepis* mainly by the n. profundus" (p. 491).

There is no doubt that in many adult Urodela, such as

Salamandra, which Jarvik took as his example for the group (Francis, 1934), the maxillaris V terminates in the orbit, as Jarvik has suggested is the case in *Porolepis.* But in many aquatic Urodela and in the larva of *Salamandra,* in which the lateral line system is retained, the lateral line nerve — ramus buccalis lateralis VII — is bound into a "truncus infraorbitalis" with the maxillaris V nerve. This compound trunk passes anteriorly right into the snout region, carrying the maxillaris V further anteriorly than in the terrestrial Urodela. It has often been supposed that the Rhipidistia resembled, in their anatomy, the larvae of Amphibia more strongly than they resembled adult forms. If, therefore, any traces of the ramus buccalis lateralis VII nerve are to be found in the porolepid Rhipidistia then the possibility cannot be excluded that the ramus maxillaris V was also present.

18. "In *Eusthenopteron* the r. buccalis lateralis passes forwards in the pons nariochoanalis laterally to the choana, giving off branches to the neuromasts of the anterior parts of the infraorbital sensory canal. It terminated far anteriorly near the very tip of the snout. In *Porolepis* it presumably broke up into several terminal branches while still in the orbit. One of these terminal branches, which supplied the foremost neuromasts of the infraorbital sensory canal, went forwards through the orbitorostral passage medially to the choana" (p. 491, cf. Jarvik, 1962).

Kulczycki (1960) has queried Jarvik's restoration of the orbitorostral passage in *Porolepis.* In *Ectosteorhachis* the nerve may possibly have passed through the dermal bones of the snout rather than between these bones and the nasal capsule as is the case in *Eusthenopteron.* Knowledge of the exact arrangement of the ramus buccalis lateralis in Rhipidistia is far from satisfactory.

20. "The r. palatinus VII in *Eusthenopteron* pierced the anterolateral part of the vomer and during this part of its course it broke up into three branches . . . In *Porolepis* the r. palatinus VII probably did not divide during its passage through the vomer . . ." (p. 492).

The ramus palatinus VII did not branch during its passage through the vomer in *Ectosteorhachis.* In this genus, as in *Porolepis,* the nerve ran through the medial part of the vomer.

21. Point 21 deals with the fact that Jarvik found traces of fusion between the tip of the palato-quadrate and the socket

for it in the endocranium, in *Eusthenopteron* but not in *Porolepis* (p. 492).

In *Ectosteorhachis*, as noted by Romer (1937, p. 22), the notch for the reception of the palato-quadrate is not lined by periosteal bone, and thus in this respect *Ectosteorhachis* agrees with *Eusthenopteron*.

22. Point 22 states that the pineal opening, between the "frontal" bones (parietal bones) is characteristically present in "*Eusthenopteron* and other Osteolepiformes" but is absent in Porolepiformes.

In the family Osteolepidae the pineal opening is present in *Osteolepis* and other Devonian forms, but absent in *Megalichthys* and *Ectosteorhachis*.

23. "The vomers in *Eusthenopteron* meet anteriorly in a median suture but their long posterior processes diverge and are separated from one another by the parasphenoid. Each vomer is provided with a descending tooth-bearing lamina. The vomers in *Porolepis* lie mainly in front of the parasphenoid. Their posterior parts are close to one another, but further anteriorly they diverge strongly. They have neither a posterior process nor a descending tooth-bearing lamina" (p. 492).

The vomers of *Ectosteorhachis*, *Megalichthys*, *Glyptopomus*, and probably also *Osteolepis* and *Thursius* (all osteolepids) lack the posterior process of *Eusthenopteron* (Thomson, 1964); the vomers in each of these genera lie anterior to the parasphenoid. It seems quite possible, although not all genera are yet well enough known, that the posterior process of the vomer is a special characteristic of the Rhizodontidae.

The vomers of *Ectosteorhachis* but not *Megalichthys* have an anterior tooth-bearing lamina comparable to that of *Eusthenopteron.*

Discussion of the vomers is closely tied up with the next subject — the nature of the parasphenoid.

24. "The parasphenoid in *Eusthenopteron* is narrow and goes forward underneath the ethmoidal region practically to the transition between the internasal wall and the divisio prenasalis communis. The parasphenoid in *Porolepis* is broad and hardly extends forwards onto the lower face of the ethmoidal region" (pp. 492-493).

In the family Osteolepidae a transition may be seen from *Osteolepis* through *Megalichthys* to *Ectosteorhachis* in which the tooth-bearing median ridge of the parasphenoid becomes progressively shorter[1] (cf. Thomson, 1964). One very likely explanation of the difference between the relative arrangements of the vomers and parasphenoid in "Porolepiformes" and "Osteolepiformes" is that their disposition on the anterior part of the palate is determined by the extent of the anterior palatal recesses which, as noted above, reflect in their turn the nature of the anterior dentition of the lower jaws.

In the "Porolepiformes" the anterior palatal recesses are large and extend posteriorly between the vomers and the parasphenoid, hence separating the vomers from one another and from the parasphenoid and limiting the anterior extent of the latter. With the evolution of the Osteolepidae (which temporally and structurally precede the Rhizodontidae), the anterior dentition of the lower jaws changed from a pair of symphysial tooth whorls (cf. Jarvik, 1962) to a set of simple tusks. Attendant upon the reduction of the anterior palatal recesses to a (paired) recess wholly anterior to the vomers and the tip of the endocranium, the parasphenoid came to extend to the tip of the palate and the vomers were free to extend medially to meet each other and the tip of the parasphenoid. In the Rhizodontidae the parasphenoid remained long and the vomers further became extended posteriorly on either side of it. In the later Osteolepidae the tooth-bearing ridge of the parasphenoid became secondarily reduced (cf. *Megalichthys* and *Ectosteorhachis* in Thomson, 1964). The vomers in the Osteolepidae do not seem to have become as strongly developed mesially as in Rhizodontidae; the vomers of *Megalichthys* and *Ectosteorhachis* retain an approximately triangular shape — with their "apices" directed mesially.

As noted by Romer (1937), the parasphenoid of *Ectosteorhachis* is in two parts, a narrow, median tooth-bearing lamina and a broad thin flange of bone spreading anterolaterally from the tooth-bearing ridge. The whole is fused to the endocranium. Unfortunately, it has not been possible to determine whether this condition is present in other "Osteolepiformes."

25. "The fossa apicalis, intervomerine pit and intervomerine canal present in *Eusthenopteron* are all absent in *Porolepis*" (p. 493).

The intervomerine pit is the anterior opening of the intervomerine canal which in *Eusthenopteron* opens into the median part of the anterior palatal recess. In *Ectosteorhachis*, as in *Porolepis*, the vomers do not meet in a median suture and thus no canal passing between them may be seen in the fossils. The significance of the intervomerine canal is unknown; it may have contained a nerve, vessel, or duct of some kind.

---

[1] The specimen of "*Thursius?*" figured by Jarvik (1942, fig. 62B) seems to fit into this series between *Osteolepis* and *Megalichthys*.

There are obvious limitations to the conclusions that can be drawn from a study of the snout apparatus alone; a broader study of the entire anatomy of the Rhipidistia might lead to results very different from those derived from this restricted series of data. Bearing in mind these limitations, however, it is permissible to reach some interim conclusions as to the relationships of the rhipidistian families to each other and to the tetrapods, from the evidence of the snout anatomy.

In the preceding discussion of the evidences for Jarvik's theory of a basic division of the Rhipidistia, the results of comparative studies seem to show that very many of the characteristics used by Jarvik to distinguish the "Porolepiformes" from the "Osteolepiformes" no longer support such an hypothesis. However, a limited number of the differences which he claimed are either corroborated by the comparative evidence or were not able to be compared in the material available for study. Thus the following features must still be considered as evidence for Jarvik's theory:

1. There seems to be a difference in the composition of the lamina nario-choanalis.
2. There are differences in the courses of certain blood vessels and minor nerve branches. However, the evidence concerning most of these is in rather an unsatisfactory state, especially for *Porolepis*.
3. A more distinct difference in the nervous system is that in *Eusthenopteron* and *Ectosteorhachis* the ramus ophthalmicus superficialis VII was seen to pass through the tectum nasi, whereas in *Porolepis* this nerve enters the nasal cavity.
4. There seems to be a trend towards lack of mobility of the palatal articulation of the palato-quadrate complex. In both the osteolepid *Ectosteorhachis* and the rhizodontid *Eusthenopteron* the notch in the palate for the reception of the pars autopalatina is not lined with periosteal bone, whereas in *Porolepis* it is.

To these few differences in the nasal region may be added certain features which fall outside the scope of the present study. Jarvik (1962) has described differences in the structure of the branchial arch apparatus of *Eusthenopteron* and *Glyptolepis*. Investigation of the branchial arch apparatus of other rhipidistians has yet to be made. Ørvig (1957) has described the microscopic structure of the scales of the Rhipidistia, and Jarvik (1962) considers that the evidence presented by Ørvig further substantiates his interpretation of rhipidistian relationships. Another feature is the difference in the nature of the anterior dentition of the lower jaws (cf. Jarvik, 1962; Thomson, 1962; and above).

In discussing the significance of the various anatomical features of the Rhipidistia, it must be borne in mind that two separate discussions are involved; on the one hand, there is the problem of the classification of the Rhipidistia themselves, and on the other hand, there is the problem of the relationship of the Rhipidistia to the tetrapods. Jarvik has endeavoured to show that these two problems are but two sides of the same coin. He delineates two basic groups of fishes in terms, principally, of their supposed anatomical relationship to the two "separate" groups of Amphibia. However, the main conclusion of the present study must be that, on the evidence of the snout anatomy, the three families of Rhipidistia investigated (Porolepidae, Osteolepidae and Rhizodontidae) are constructed according to a common anatomical plan. Furthermore, and most importantly, this overall similarity in structure is particularly manifest in the majority of those characters (the pattern of the nervous system, nature of the internasal wall, etc.) which Jarvik considered to be diagnostic of the specific relationships of the "porolepiforms" and urodeles, on the one hand, and the "osteolepiforms" and the anurans, on the other hand. Thus, from the detailed review of the comparative anatomy of the rhipidistian snout, given above, we must come to the conclusion that there is no substantial evidence in these structures to support the supposition that any particular family of Rhipidistia is more closely allied to one particular group of Amphibia than to another. There is no evidence to support the particular diphyletic theory of the origin of the tetrapods proposed by Jarvik.

We may now turn to examine Jarvik's proposition that the Rhipidistia comprise two separate stocks — "porolepiform" and "osteolepiform." We may accept the fact that the families Porolepidae and Holoptychidae are very closely allied. But to balance the apparent distinctions between these fishes and the combined Rhizodontidae and Osteolepidae, noted in the preceding paragraphs, we may take note of the very numerous resemblances between the four families of Rhipidistia — resemblances which indicate the essential unity of the group as a whole (Schmalhausen, 1959, 1960; Romer, 1962; Thomson, 1962; Szarski, 1962). Most importantly we may note that in certain features, such as the structure of the scales (Ørvig, 1957), the configuration of the nasal apparatus, and possibly also the arrangement of the vomers and parasphenoid on the palate, the Osteolepidae differ from the Rhizodontidae as greatly as they differ from the Porolepidae and Holoptychidae combined. Such considerations led Berg (1958) to consider the Rhipidistia as being made up of *three* main groups — the Porolepiformes, the Osteolepiformes and the Rhizodontiformes. Such a scheme seems more correctly to assess the interrelationships of the four families than does that of Jarvik. Assignation of ordinal rank to each group has the disadvantage of over-emphasizing the differences between the families. A more satisfactory arrangement would be to consider each group as no more than a superfamily.

In summary we may conclude:

1. That the four families of Rhipidistia are, anatomically, a close-knit assemblage.

2. The interrelationships of the Rhipidistia may not be expressed by a simple separation of "Porolepiformes" and "Osteolepiformes," but rather the Rhipidistia may be thought to comprise three superfamilies, the Holoptychoidea, Osteolepoidea and the Rhizodontoidea, of equal rank.

3. There is no evidence in the anatomy of the rhipidistian snout to indicate a diphyletic origin of the urodele and anuran Amphibia from within the Rhipidistia.

LITERATURE CITED

BERG, L. S.
1958. System der rezenten und fossilen Fischartigen und Fische. Berlin, Deutscher Verlag, 310 pp.

BRYANT, W. L.
1919. On the structure of *Eusthenopteron*. Bull. Buffalo Soc. Nat. Sci., **13**: 1-23.

COGHILL, G. E.
1902. The cranial nerves of *Amblystoma tigrinum*. J. Comp. Neurol., **12**: 205-289.

EATON, T. H.
1959. The ancestry of the modern Amphibia: a review of the evidence. Univ. Kansas Publ. Mus. Nat. Hist., **12**: 217-240.

Francis, E. T. B.

1934. The anatomy of the salamander. Oxford, 381 pp.

Holmgren, N. and E. A. Stensiö

1936. Kranium und Visceralskelett der Akranier, Cyclostomen und Fische. *In* L. Bolk *et alia,* Handbuch der vergleichenden Anatomie der Wirbeltiere, vol. 4: 345-353.

Jarvik, E.

1937. On the species of *Eusthenopteron* found in Russia and the Baltic states. Bull. Uppsala Geol. Inst., **27:** 63-127.

1942. On the structure of the snout in crossopterygians and lower gnathostomes in general. Zool. Bidrag., **21:** 237-675.

1954. On the visceral skeleton in *Eusthenopteron* with a discussion of the palato-quadrate in fishes. K. Svenska Vetens.-Akad. Handl., (4) **5:** 1-104.

1962. Les Porolépiformes et l'origine des urodèles. Colloques Internat. du Centre de la Récherche Scientifique, Paris, no. 104: 87-101.

Kulczycki, J.

1960. *Porolepis* (Crossopterygii) from the Lower Devonian of the Holy Cross Mountains. Acta Palaeont. Polonica, **5:** 65-106.

Ørvig, T.

1957. Remarks on the vertebrate fauna of the lower Upper Devonian of Escuminac Bay, P.Q., Canada, with special reference to the porolepiform crossopterygians. Arkiv. Zool., **10** (6): 367-426.

Parsons, T. and E. E. Williams

1962. The teeth of Amphibia and their relation to amphibian phylogeny. J. Morph., **110** (3): 375-390.

1963. The relationships of the modern Amphibia: a re-examination. Quart. Rev. Biol., **38:** 26-53.

Pinkus, F.

1895. Die Hirnnerven des *Protopterus annectens.* Morph. Arbieten., **4:** 275-346.

Romer, A. S.

1937. The braincase of the Carboniferous crossopterygian *Megalichthys nitidus.* Bull. Mus. Comp. Zool., **82** (1): 1-67.

1941. Notes on the crossopterygian hyomandibular and braincase. J. Morph., **69** (1): 141-160.

1955. Herpetichthyes, Amphibiodei, Choanichthyes or Sarcopterygii? Nature, **176:** 126.

1962. Vertebrate evolution: a review. Copeia, 1962 (1): 223-227.

Säve-Söderbergh, G.

1936. On the morphology of Triassic stegocephalians from Spitzbergen, and the interpretation of the endocranium in the Labyrinthodontia. K. Svenska Vetens.-Akad. Handl., (3) **16:** 1-181.

Schmalhausen, I. I.

1959. Concerning monophyletism and polyphyletism in relation to the problem of the origin of the land vertebrates. Bull. Mosk. Obshch. Isp. Pri. Biol., **64** (4): 15-33. (In Russian.)

1960. Biological basis of the classification of the crossopterygian fish. Palaeont. J. Akad. Nauk. U.S.S.R., 1960, no. **1**: 3-15. (In Russian).

STENSIÖ, E. A.
1922. Notes on certain crossopterygians. Proc. Zool. Soc. London, 1922: 1241-1271.

STERNBERG, R. M.
1941. Cranial morphology of the Devonian crossopterygian *Eusthenopteron*. Univ. Toronto Studies, Geol. Ser., no. 45: 1-48.

SZARSKI, H.
1962. Origin of the Amphibia. Quart. Rev. Biol., **37**: 189-241.

THOMSON, K. S.
1962. Rhipidistian classification in relation to the origin of the tetrapods. Breviora, Mus. Comp. Zool., no. 177: 1-12.
1964. Revised generic diagnoses of the fossil fishes *Megalichthys* and *Ectosteorhachis* (family Osteolepidae). Bull. Mus. Comp. Zool., **131**(9): 283-311.

VOROBJEVA, E. I.
1959. A new genus of crossopterygian fish — *Platycephalichthys* from the Upper Devonian of Lovat. Palaeont. J. Akad. Nauk. U.S.S.R., 1959, no. 3: 95-106. (In Russian.)
1960a. New facts about the genus *Panderichthys* from the Devonian of the U.S.S.R. Palaeont. J. Akad. Nauk. U.S.S.R., 1960, no. 1: 87-96. (In Russian.)
1960b. Concerning the systematic position of *Eusthenopteron wenjucovi* (Rohon). Palaeont. J. Akad. Nauk. U.S.S.R., 1960, no. 2: 121-129. (In Russian.)

WATSON, D. M. S.
1926. The evolution and origin of the Amphibia. Phil. Trans. Roy. Soc. London, (B) **214**: 189-257.

WATSON, D. M. S. and H. DAY
1916. Notes on some Palaeozoic fishes. Mem. and Proc. Manchester Lit. Phil. Soc., **60** (1): 1-47.

ABBREVIATIONS USED IN THE FIGURES

a.cut.va.	anterior cutaneous artery
a.m.r.	anterior median recess
ana.	anterior nasal artery
a.p.r.	anterior palatal recess
a.pr.	anterior postrostral
a.r.	anterior rami (of profundus)
c.ana.	canal for anterior nasal artery
cc.aa.	canals through anterior nasal wall
cc.mea.	canals for median ethmoid arteries
ch.	choana
c.l.	crista lateralis
c.l.cut.va.	canal for lateral cutaneous artery

c.lat.	canal for lateral nasal vein
c.l.l.	lateral line canal
c.max.	canal for maxillary V nerve
c.m.cut.va.	canal for median cutaneous artery
c.mev.	canal for median ethmoid vein
c.o.s.	canal for ramus ophthalmicus superficialis VII
c.pal.	canal for palatine VII nerve
c.pr.V	canal for profundus V nerve
c.r.ext.	canal for ramus exterior (of profundus)
c.ros.VII	canal for ramus ophthalmicus superficialis VII.
c.r.r.	canal for ramus rostralis (of profundus)
ds.	dermosphenotic
e.n.	external naris
f.ap.	foramen apicale
f.cut.va.	foramen for medial cutaneous artery
ff.ros.	foramina for ramus ophthalmicus superficialis VII
gr.c.l.	groove on medial face of crista lateralis
gr.prf.	groove for profundus nerve
gr.ros.	groove for ophthalmicus superficialis VII
g.s.o.l.	groove for supraorbital lateral line
i.c.a.	internal carotid artery
i.o.c.	canal for infraorbital lateral line
i.o.l.	infraorbital lateral line
l.c.v.	lateral canal in vomer
l.cut.a.	lateral cutaneous artery
l.n.v.	lateral nasal vein
m.c.v.	medial canal in vomer
mea.	median ethmoid arteries
mev.	median ethmoid veins
m.pr.	median postrostral
n.	nasal
n.c.	nasal cavity
n.pq.	notch for palato-quadrate
n.prf.	notch for profundus nerve
n.ros.	notch for ramus ophthalmicus superficialis
n.r.p.	naso-rostro-premaxilla
n.t.	tube of external naris
olf.c.	connection of anterior cutaneous artery back to canal for olfactory tract
olf.t.	olfactory tract
pa.	parietal
pal.a.	palatine artery
pin.f.	pineal foramen
pm.t.	premaxillary tusk
p.n.	postnarial
p.q.	palato-quadrate
p.rec.	posterior median recess

prf.	profundus V nerve
pr.n.	prenarial
p.v.f.	parasphenoid
ps.	posteroventral fenestra
r.ext.	ramus exterior (of profundus)
r.ln.	ramus lateralis narium (of profundus)
r.max.	ramus maxillaris V
r.mn.	ramus medialis narium (of profundus)
ros.	ramus ophthalmicus superficialis VII
r.pal.	ramus palatinus VII
r.r.	ramus rostralis (of profundus)
rr.a.	anterior rami (of profundus)
s.o.l.	supraorbital lateral line
v.	vomer

(Received May 10, 1963)

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 11

THE ANOLES (SAURIA, IGUANIDAE) OF THE GUADELOUPÉEN ARCHIPELAGO

By James D. Lazell, Jr.

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
September 15, 1964

PUBLICATIONS ISSUED BY OR IN CONNECTION WITH THE

MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

BULLETIN (octavo) 1863 — The current volume is Vol. 131.

BREVIORA (octavo) 1952 — No. 207 is current.

MEMOIRS (quarto) 1864–1938 — Publication terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 41 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 28 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained from the Publications Office of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Peters' Check-List of Birds of the World. Volumes 1, 4 and 6 are out of print; volumes 2, 3, 5, 7, 9, 10 and 15 are currently available.

Phylogeny and Evolution of Crustacea. Proceedings of a conference held at Cambridge, Mass., March 6-8, 1962. H. B. Whittington and W. D. I. Rolfe, editors. Cambridge, Mass., 192 pp., 80 figs., 1963. Cloth bound, $6.75.

Fishes of the Gulf of Maine, by Henry B. Bigelow and William C. Schroeder. Washington, viii - 577 pp., 1953. Photo-offset reprint, $6.50.

PUBLICATIONS OF THE BOSTON SOCIETY OF NATURAL HISTORY

The remaining stock of the scientific periodicals of the Boston Society of Natural History has been transferred to the Museum of Comparative Zoology for distribution. Prices for individual numbers may be had upon request.

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 11

THE ANOLES (SAURIA, IGUANIDAE) OF THE GUADELOUPÉEN ARCHIPELAGO

By James D. Lazell, Jr.

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
September, 1964

Bull. Mus. Comp. Zool., Harvard Univ., **131**(11):359-401, Sept., 1964

No. 11 — *The Anoles (Sauria, Iguanidae) of the Guadeloupéen Archipelago*[1]

By James D. Lazell, Jr.

INTRODUCTION

The archipelago which lies between Dominica and Montserrat in the northern portion of the Lesser Antillean chain represents both a political and a geographical unit. Part of the French West Indies, and of the Republic of France, it is comprised of four large islands — La Guadeloupe (often, though erroneously, called "Basse-Terre" for its capital city) Grande Terre, La Désirade, and Marie Galante — and a number of smaller islands: Ilet-à-Kahouanne, Ilet-à-Fajou, Ilet-à-Cochons (ou Gouvernement), plus two island groups, Les Iles da la Petite Terre, and Les Iles des Saintes. Taken together, these islands may be referred to as the Guadeloupéen archipelago, namd for La Guadeloupe, the largest of them.

The Guadeloupéen archipelago is not a geological unit. La Guadeloupe itself, about 25 miles long and 15 miles wide, contains a central spine of mountains that reach nearly 5,000 feet (1,467 meters) above sea level. Many of these mountains are still actively volcanic, and attest to the process which has built this land mass. Grande Terre, on the other hand, though nearly as large in area, is low, rather flat throughout, and comprised of oceanic limestone overlying an ancient volcanic base. Following Davis (1926), La Guadeloupe may be taken as representative of the "first cycle" islands of the Lesser Antilles, and Grande Terre as representative of the "second cycle" islands.

The first cycle islands are composed of volcanic rock and have never been submerged and recapped with limestone. Along with La Guadeloupe, Les Iles des Saintes and Ilet-à-Kahouanne are members of this group; Les Iles des Saintes and Ilet-à-Kahouanne are, however, no longer actively volcanic, and are the severely eroded remnants of once larger land areas. The latter islands may be considered as among the oldest remaining in the first cycle.

The second cycle islands, though of volcanic origin, have subsequently been submerged and capped with limestone. Grande Terre, Ilet-à-Cochons, La Désirade, Les Iles de la Petite Terre, and Marie Galante, taken together, constitute the southernmost limit of the second cycle in the Lesser Antilles. There is no information available to me on their relative ages.

---

[1] The Anoles of the Eastern Caribbean. Part VII.

Ilet-à-Fajou is in reality an extensive mangrove swamp. It lies in the shallow Grande Cul-de-Sac Marin, and appears to be a product of the predominant northeast wind: a collection of detritus banked up along a strip of coral reef. Its northern edge is a few meters above sea level, and is, even during the rainy season when I was there, a dusty bit of barren desert. Squeezed between this small area of desert and the sea is a narrow band of scrub and thornbush where the anoles of Ilet-à-Fajou are to be found.

In general, *Anolis* are found throughout the archipelago wherever more than herb-stage vegetation occurs; they are not, however, apparently found on the highest peaks of La Guadeloupe. In the last revision of Lesser Antillean *Anolis*, by Underwood (1959), the five named taxa of the Guadeloupéen archipelago were reviewed; *marmoratus*, *ferreus*, and *speciosus* (with two subspecies) were considered distinct at the species level from other *Anolis* of the *bimaculatus* species group. A fifth form, *alliaceus*, was considered to be a subspecies of *bimaculatus* itself (the type locality of *bimaculatus* is St. Eustatius, separated by four islands on three banks and several hundred miles from the Guadeloupéen archipelago), and a sixth form, the Désirade anole, was granted specific status, but not described and named. In his discussion of *alliaceus*, Underwood (p. 200) notes that Williams regarded that form, *sensu* Underwood, to be a composite of two distinct species. Therefore, Underwood had available to him at the time of his revision representatives of a maximum of seven taxa from five islands of the archipelago.

The salient features of Underwood's revision may be summarized as follows: he regarded assignment to species or subspecies level of isolated, allopatric forms to be largely a matter of taste; he believed color characters to be of primary importance in species recognition, and squamation characters to be "only indirectly significant by-products of species differentiation" (p. 193); he preferred to regard populations as subspecies when monophyletic relationship was "clear"; and finally, he believed that the general degree of morphological similarity and difference between two forms could be used as a reasonable indication of the clarity of their relationship.

Although I do not feel that there was consistent adherence to these principles in the annotated list of forms of the eastern

Caribbean presented by Underwood, the material he had available was extremely scant, to say the least, and it is therefore only to his last principle that I take exception at this point.

The validity of "degree of similarity" as an indication of relationship needs especial consideration before it can be used in the species group. In particular, it is demonstrably invalid with regard to sympatric species of *Anolis* in the West Indies. An example of this point can be found in Underwood and Williams (1959) with respect to the *grahami-opalinus* group in Jamaica: here Underwood (p. 47) himself acknowledges that the two intergrading subspecies of *Anolis grahami* are, in fact, considerably more morphologically divergent from each other than either is from the sympatric *Anolis opalinus*.

To me it seems that a principle such as "degree of similarity," so easily rejected for sympatric forms, should not be considered valid when applied to allopatric forms in the species group. "Degree of similarity" is in constant use with higher taxonomic categories, but one is reminded of Simpson's (1961) discussion of the fact that higher taxonomic categories are entirely man-made assemblages, and therefore of a wholly arbitrary nature. Morphological "degree of similarity" has, for these reasons, not been used in the following revision and description of Guadeloupéen *Anolis* as an indication of specific or subspecific rank. Acceptance of the "principle" would lead to the wrong conclusions in more than half the cases considered.

In revising the Guadeloupéen forms, and describing the previously unknown ones, I have used instead Simpson's definition of the "evolutionary species," in which the principal criterion is continuity of evolutionary role.

As Simpson carefully points out, geographic isolation tends to break the continuity of evolutionary role; thus isolated, allopatric forms may well be distinct species, even when derived from the same ancestor. In assigning populations to subspecific rank under the same species, in the Guadeloupéen archipelago, I admit the following as evidences of continuity of evolutionary role:

1. Actual intergradation: where there exists between two distinct populations occupying different geographic areas a zone in which "intergrade" individuals assure continuous gene flow between the two extremes.

2. The presence of a morphologically intermediate population,

when isolated by a topographical barrier, between the two extremes. This would include a series of geographically isolated, allopatric[1] populations which proceed in a stepwise sequence relative to the development or degeneration of characters in such a way that the second is intermediate between the first and third, the third is intermediate between the second and fourth, etc. — *even when the forms involved are 100 per cent distinct from each other.* A sequence of forms such as this will be referred to hereafter as a ''stepped-cline'' series, and in such cases I regard each member of the series as worthy of nomenclatural recognition providing it is diagnostically distinct from the others. In cases where it is not diagnostically distinct from the others I refer to it as though it were a population of actual intergrades.

3. Tenable evidence that the extant differences are the result of a trend in an isolated population of the species under which the different form is to be included. A case like this requires, to my way of thinking, the presence of some third population which, though demonstrably a member of the species involved on other bases, sets a precedent for evaluation of the sort of differences noted in the form presumed to have resulted from this trend. Examples of this are comparatively rare, and, I believe, constitute the only cases in which assignment to rank may degenerate to a matter merely of personal taste.

It is my belief, based on seven years of observing West Indian *Anolis*, both in the field and in the laboratory, that no two samples of specimens, no matter how different they appear, may be unfailingly allocated to correct rank relative to each other within the genus unless they are sympatric, or unless samples of geographically intermediate populations are available and considered. In the latter case, it must be remembered that, should the samples be found to represent members of the same evolutionary species, their status as distinct subspecies will depend entirely on whether or not they represent diagnostically homogeneous, clear-cut geographic segments of the same species. Two ends of a gradual cline, not broken into segments, or whose segments are not diagnostically distinct, are not herein regarded as nomenclaturally distinct, no matter how different from each other.

This is to say that *a great deal of geographic variation within species does not produce the sort of segmental units we can*

---

[1] The term "allopatric" is here used *sensu stricto*, and is not to be confused with "parapatric."

usefully refer to as "subspecies." The fact that a large number of geographic units which can be usefully regarded as subspecies are present in the Guadeloupéen archipelago is genuinely remarkable, and is considered under "Evolutionary Discussion."

METHODS OF ANALYSIS

The primary materials for this study are 792 specimens of *Anolis* collected from 77 localities on 13 islands throughout the archipelago. During August and September of 1961, 755 specimens were collected from 73 localities, and the additional 37 specimens from four localities were collected in September of 1962 on two islands, to insure coverage of all distinctive populations. Specimens already in the Museum of Comparative Zoology (MCZ) were considered only after the living material had been examined.

Specimens were preserved, tagged, and catalogued only after careful color notes had been taken. Color sketches were made in the field of all the forms involved. All of the forms described herein were initially recognized on the basis of color characters. Scale characters, though often noticeable in the field, were not considered in detail until the specimens were studied in the laboratory. Fortunately, those characteristics of squamation which were noted in the field, as well as others discovered since, vary concordantly with the color characters, and are helpful in distinguishing the forms.

In attempting to render the females of the various forms more readily distinguishable, I have classified the middorsal patterns represented among female Guadeloupéen *Anolis* under five headings (see Figure 1):

1. *Broken:* A pale middorsal stripe set off from the dorsolateral coloration by a coalescing series of dark spots.
2. *Striped:* A pale middorsal stripe set off by a continuous dark border on each side.
3. *Ladder:* A middorsal pattern with dark transverse connections across the pale middorsal stripe from one border to the other.
4. *Mottled:* Light and dark middorsal markings not forming a special pattern.
5. *Obsolete:* A dark middorsal zone, without markings, contrasted to the dorsolateral coloration.

It was noted in the field that the females of the forms involved were not only distinctive relative to each other, but that the

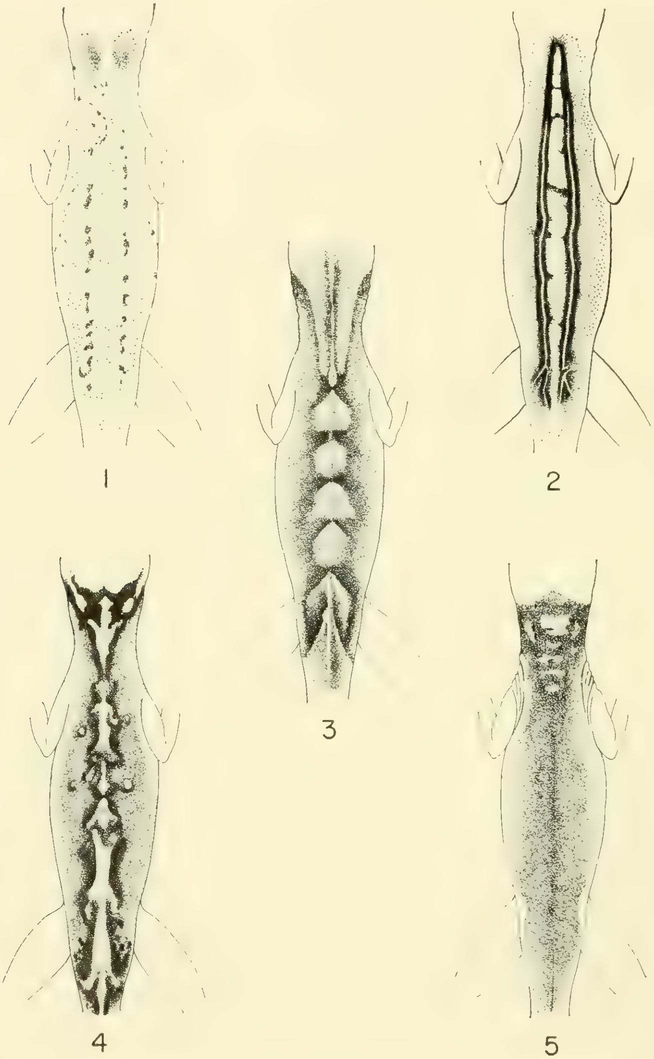


Figure 1. Middorsal patterns of female *Anolis marmoratus:* 1. broken (MCZ 71284); 2. striped (MCZ 70945); 3. ladder (MCZ 70676); 4. mottled (MCZ 71356); 5. obsolete (MCZ 71210). See text for explanation.

total coloration and pattern of the females was often more constant within any one taxon than these features in the males. Underwood did not deal with females simply because he regarded them as being only occasionally distinctive. I have not found this to be the case; on the contrary, the females in life are just as distinctive as the males. Also, males of some forms, from any one locality, are apt to show such a bewildering array of spots and marbles, varying from many and bold to very few and vague, that they can be genuinely confusing until one has come to recognize the constant, and often rather subtle, characters common to all specimens. Females were not found to differ from males with respect to squamation characters.

The following general characteristics of squamation were considered for all forms:

1. *Scale size.* That striking differences in scale size existed between several of the forms was noted in the field. In an attempt to render this character diagnostically useful, several methods of quantification were used. First, the number of dorsals in the standard distance (defined as the distance from the center of the eye to the tip of the snout) was counted and plotted against the number of ventrals in the standard distance in a two-variable linear graph. This method showed the differences anticipated, but was open to the criticism that head-body proportions might vary among the several forms. Consequently, the ratio of standard distance to snout-vent length was calculated for all specimens. The relationship proved quite constant: the standard distance is between 16 and 19 per cent of the snout-vent length in all Guadeloupéen anoles, except very old and very young specimens; in these exceptions the standard distance may be as little as 14.5 per cent of the snout-vent length. As a further check on the accuracy of the standard distance count method, the around-the-body count approach was utilized. Around-the-body counts, midway between axilla and groin, were made on all specimens from Ilet-à-Kahouanne, Ilet-à-Fajou, Les Iles de la Petite Terre, Marie Galante, and Les Iles des Saintes, as well as in scattered series from various localities on La Guadeloupe, Grande Terre, and Désirade: some 220 in all. This method showed the same differences between the same forms, and was sufficiently tedious to increase my appreciation of the practical value of the standard distance count.

In the following diagnoses of each form, the range of dorsal scales counted in the standard distance, based on all the specimens available from my collections, is given. The count is made between six and eight scales lateral to the middorsal line, and

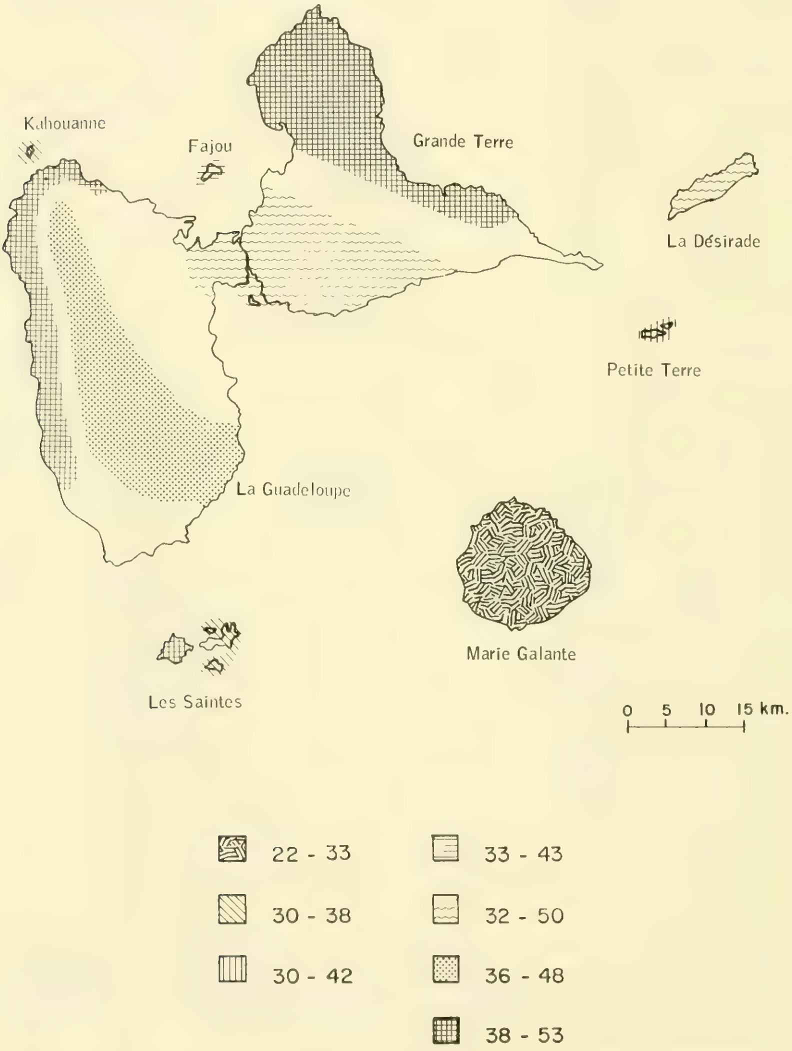

Kahouanne
Fajou
Grande Terre
La Désirade
Petite Terre
La Guadeloupe
Marie Galante
Les Saintes
0 5 10 15 km.
22 - 33
30 - 38
30 - 42
33 - 43
32 - 50
36 - 48
38 - 53

Figure 2. Geographic variation in number of dorsal scales contained in the standard distance at midbody. The major islands and island groups are here named for future reference.

parallel to that line. In each case the average for all the specimens counted was not more than ± 1 from the mean of the range given. Making the count in the manner outlined renders what might have been a most laborious sort of character as simple as possible, and yet shows quite well the differences noted between forms. (See Figure 2.)

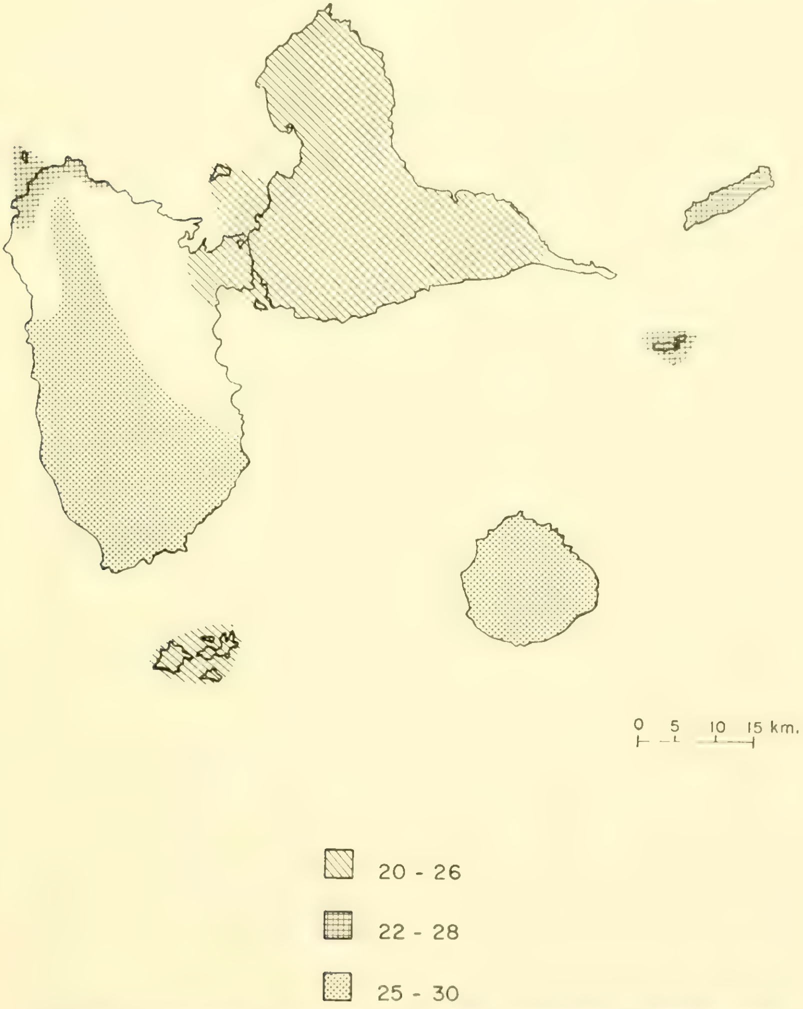


Figure 3. Geographic variation in number of subdigital lamellae under second and third phalanges of fourth toe. The major islands and island groups are named in Figure 2.

2. *Subdigital lamellae:* Lamellae were counted under the second and third phalanges of the fourth toe. The differences are averages, and not diagnostic, but the geographic variation with respect to this character has been mapped because the variation is real and concordant with the variation in other characters. (See Figure 3.)

SYSTEMATIC DISCUSSION

Underwood recognized five named populations and one unnamed one as representatives of five distinct species, one with two subspecies; Williams would have added a sixth. In the present review all of those names regarded as valid by Underwood are retained, the Désirade anole he felt he could not properly name is described, and Williams' seventh form is accepted and described. I have, however, lowered all of them to subspecific rank under the same species. So that I may not immediately be scorned as a rabid lumper, let me point out that I have likewise described five more subspecies of the same species, making in all twelve subspecies.

Anolis marmoratus Duméril and Bibron, 1837, is the oldest available name for a Guadeloupéen anole. *A. marmoratus* may be distinguished from the adjacent forms by the following brief, species-level diagnoses:

Anolis oculatus, of Dominica, is an anole of the *bimaculatus* group, *sensu* Underwood, in which the prenasal scale borders on the rostral anteriorly and the anterior edge of a large nasal scale (entirely containing the naris) posteriorly; the prenasal is roughly quadrangular in shape. The ventrals are always at least faintly keeled, and the keels form lines that converge on the ventral midline posteriorly.

Anolis marmoratus, of the Guadeloupéen archipelago, is an anole of the *bimaculatus* group, *sensu* Underwood, in which the prenasal scale borders the rostral directly, extends posteriorly to or beyond the level of the anterior edge of the naris, and either borders the anterodorsal edge of the nasal, or itself forms the anterodorsal border of the naris. The ventrals may or may not be keeled, but if keeled at all the keels form lines converging towards (rarely ever reaching) the ventral midline, or parallel to it.

Anolis lividus, of Montserrat, is an anole of the *bimaculatus* group, *sensu* Underwood, in which the prenasal scale borders directly on the rostral, extends posteriorly to or beyond the level

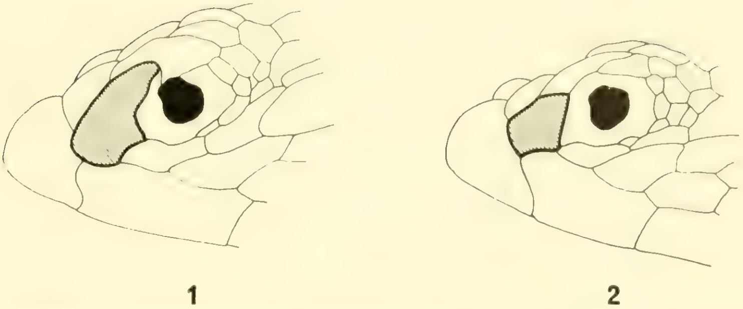


Figure 4. Snout squamation in two species of *Anolis:* 1. *A. marmoratus* (MCZ 71202); 2. *A. oculatus* (MCZ 60364). The prenasal scale is shaded.

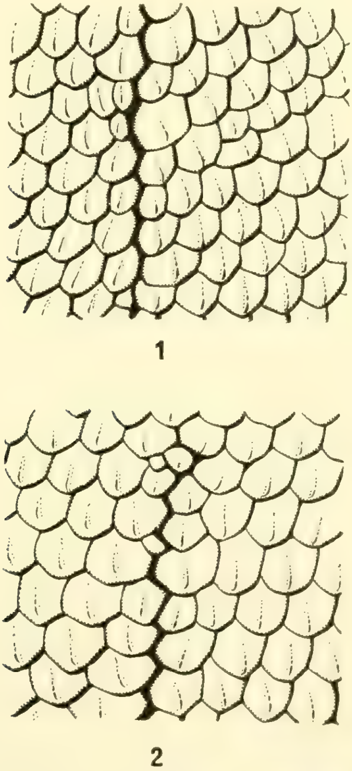


Figure 5. Ventral keeling in two species of *Anolis:* 1. *A. lividus* (MCZ 6176); 2. *A. marmoratus* (MCZ 71202). In *A. marmoratus* the ventrals may be entirely smooth.

of the anterior edge of the naris, and either borders on the anterodorsal edge of the nasal, or forms the anterodorsal border of the naris itself — as in *A. marmoratus.* The ventrals are always at least faintly keeled, and while many lines of keels may converge on the ventral midline posteriorly, at least some, in the abdominal area, form lines which diverge.

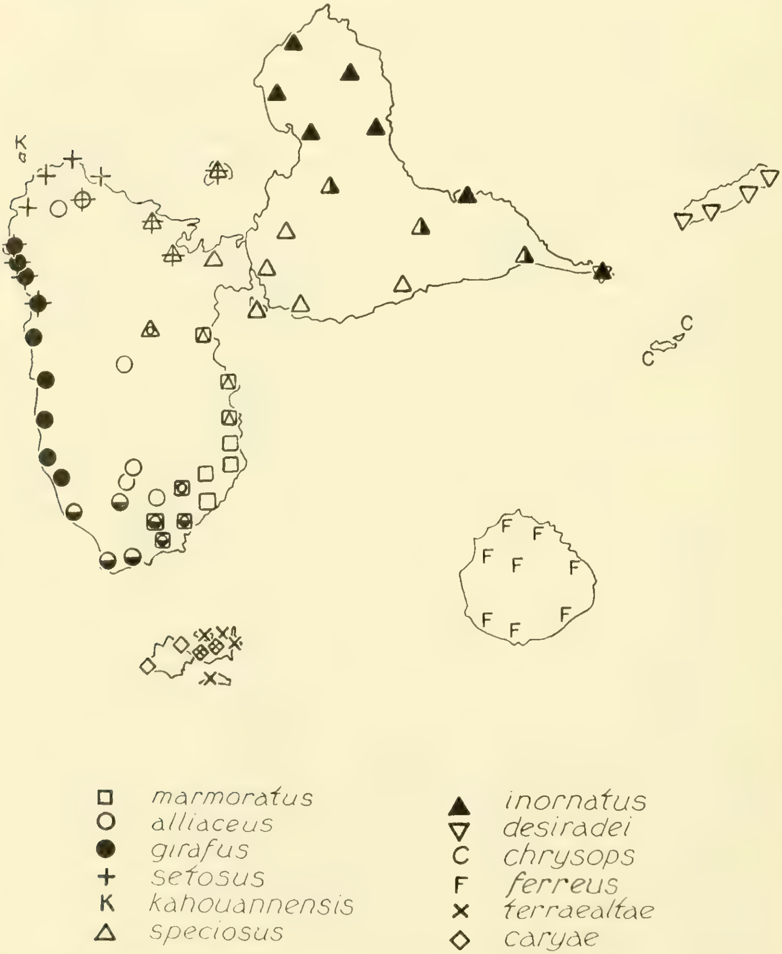

K
C
C
F
□ marmoratus
○ alliaceus
● girafus
+ setosus
K kahouannensis
△ speciosus
▲ inornatus
▽ desiradei
C chrysops
F ferreus
× terraealtae
◇ caryae

Figure 6. The ranges of the twelve forms of *Anolis marmoratus* in the Guadeloupéen archipelago. The major islands and island groups are named in Figure 2.

Figure 4 shows both conditions of the prenasal scales, and Figure 5 shows examples of the most confusing sorts of abdominal keeling. Using these characteristics, the three species may be separated without too much difficulty, regardless of age or sex. I have seen some specimens in which the prenasal was equivocal on one side, but it was always definitely one sort or the other on the other side, and provided the correct identification.

The ranges of the twelve forms recognized are mapped in Figure 6.

The nominate form of the Guadeloupéen species is:

ANOLIS MARMORATUS MARMORATUS Duméril and Bibron

Anolis marmoratus Duméril and Bibron, 1837, Érp. Gén. 4: 139.

Holotype: Muséum National d'Histoire Naturelle Ig. 43, no date, coll. Plée.

Type locality: "Martinique" (in error); herein revised to Capesterre, La Guadeloupe.

Diagnosis: Dorsal scales in the standard distance 36 to 48 (average 42); 25 to 30 (average 28) subdigital lamellae; adult male green, changing to brown; snout suffused with orange; head, neck, and orbital area boldly marbled with bright orange; throat fan light orange-yellow with yellow scales. Adult female green, with an obsolete middorsal pattern.

Description: MCZ 71202 is noted in my field catalogue as "the most beautiful anole I have ever seen." In life, this adult male was bright apple-green, shading to blue on the tail and yellow-green on the limbs. No flank stripe was present. On the neck and head the ground color shaded to blue-grey; the snout and head were broadly suffused with russet becoming in the temporal, orbital, and nape regions brilliant orange marbles, tending towards longitudinal stripes. The belly was lime-green. The throat fan was bright, pale orange-yellow with butter-yellow scales. In the dark phase the specimen assumed a deep chocolate-brown dorsally, became much darker ventrally — even to the extent of darkening the throat fan — but retained the orange marbling. Aside from the marbling on the head and neck, there were no markings. This specimen, the largest examined, was 77 mm in snout-vent length.

The adult female is grass-green, shading to grey or grey-brown on the head, middorsum, and tail, and with a lime-green belly. Aside from the contrast between the green of the sides and the grey to grey-brown of the middorsum, producing the pattern I have termed "obsolete," there are no markings in life. Color change is merely from darker to lighter.

Variation: The extent of marbling varies in the adult male from all over the head and neck, to or beyond the level of the shoulder (as in the holotype), to restriction to the head region only. The suffusion of orange pigment anterior to the eyes, however, is constant in all, and the lack of it will serve to distinguish intergrades with other forms which may also show orange marbling. The ground color of the head varies from slatey blue-grey to powder blue-grey.

Distribution: This form is restricted to the plain of Capesterre, southwestern La Guadeloupe.

Specimens examined: MCZ 56043, "Guadeloupe" (Guesde coll.); MCZ 71179-93, Capesterre; MCZ 71194-201, Bananier; MCZ 71202-12, Routhiers; MCZ 71213-22, Carangaise.

Discussion: This spectacular anole has very narrow areas of intergradation to the west and south with the montane form and intermediates between the montane form and the southern leeward coast form. To the north, however, there is little barrier or ecological break, and a lengthy zone of intergradation with *speciosus* extends along the coast. MCZ 71140-43, from Grande Etang, *ca.* 400 meters elevation, are intergrades with *alliaceus,* the montane form. MCZ 71150-61 from Dolé, MCZ 71172-78 from Morne-à-Zailes, and MCZ 71162-71 from Trois-Rivières represent three-way intergrades between *marmoratus, alliaceus,* and the southern leeward coast form, *girafus.* MCZ 71136-39 from Ste. Marie, MCZ 71128-35 from Goyave, and MCZ 71113-27 from Petite Bourg represent intergrades with *speciosus,* which occupies the "waist" between La Guadeloupe and Grande Terre as well as southwestern Grande Terre.

ANOLIS MARMORATUS ALLIACEUS Cope

Anolis alliaceus Cope, 1864, Proc. Acad. Nat. Sci. Philadelphia, 175. Type: British Museum of Natural History (BMNH) 946. 8.28.96, no collector, no date.

Anolis bimaculatus alliaceus, Underwood, 1959, p. 199.

Type locality: None designated; here restricted to Maison Forestier du Matouba, elevation 700 meters, La Guadeloupe.

Diagnosis: Dorsals in the standard distance 36 to 48 (average 42); 25 to 30 (average 28) subdigital lamellae; adult male green with no blue or bluish pigment in this ground color;

palpebral area of orbit white in the light phase, changing to grey as the animal turns dark green; dark dots, tending to run together, scattered over the anterior and dorsal surfaces, and set off by pale cream borders; throat fan deep orange with green scales. Adult female green with mottled middorsal pattern and small light or dark dots anteriorly.

Description: An adult male, MCZ 71340, from the type locality, was pea-green and completely lacked the bluish tones apparent on the posterior body or tail in males of all other forms from La Guadeloupe. The orbital area was brown-green, but the edges of the lids (palpebral area) were white. Large blue-black dots, some running together to form short marbling, were present dorsally; these dots were set off by cream-yellow areas that blended abruptly into the pea-green ground color. A vague, cream-yellow flank stripe was indicated across the forelimb insertion. Dull yellowish green on the temporal region extended posteriorly to beyond the ear, and was set off by a dark brownish streak along the upper mandible and a similar streak through the eye. The throat fan was dark, dull orange with yellowish green scales. The belly was bright green. Color change involved a darkening of the ground color, obscuring the head streaking, but intensifying the contrast between the ground color and the cream-yellow borders of the dots. This specimen, the largest examined, measured 72 mm snout to vent. (See Figure 7.)

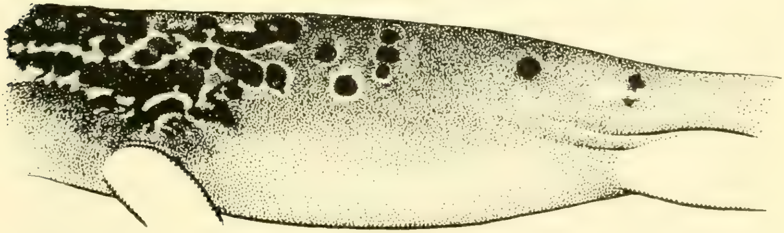


Figure 7. A representative pattern in adult male *Anolis marmoratus alliaceus* (MCZ 71340).

The adult female, in life, is duller green than the male, and shows a middorsal pattern of light and dark mottlings. Spots, small and sometimes indistinct, of dark or light pigment are present on the anterior trunk. The head streaking is usually present and notable.

Variation: The extent of dotting is extremely variable; some specimens are dotted and marbled extensively over the posterior nape, the shoulders and anterior middorsum; other specimens show only one indistinct dot in the region of the axilla. In some specimens the head streaking is indistinct. The complete lack of blue in the ground color, and the throat fan color combination, suffice to distinguish this form invariably from other green *marmoratus* even should a completely dotless specimen be encountered. The characters noted, as well as the bright green belly, serve to distinguish this form from the only other spotted anole on La Guadeloupe, the southern leeward coast form *girafus*. There is little variation in females.

Distribution: This form is restricted to rain forest in the central highlands of La Guadeloupe. It is strikingly arboreal and therefore difficult to collect, especially in climax forest, where the trees may reach 40 meters in height. None were seen at elevations higher than 900 meters.

Specimens examined: MCZ 61078-81, Matouba, 2000 ft. (= *ca.* 600m), nr. St. Claude (Proctor coll.); MCZ 71338-46, Maison Forestier du Matouba, 700 meters; MCZ 71347-55, Trace Victor Hughes, between Matouba and Grande Decouverte, *ca.* 850 meters; MCZ 71356, Etang-as-de-Pique; MCZ 71358-60, north ridge, Morne Moustique, *ca.* 650 meters. MCZ 71357, from Morne Goton, *ca.* 650 meters, has somewhat elongate dorsal scales, reminiscent of the north coast form, *setosus*. It is otherwise typical of *alliaceus;* Morne Goton is therefore taken to be the northern limit of the range of *alliaceus*.

Discussion: Intergradation with the nominate form has been discussed under that form. The montane anole, *alliaceus,* intergrades with *speciosus* between the "waist" and the central highlands at Vernou (MCZ 71144-49). Intergrades with *setosus* of the north coast are represented by MCZ 70883-4. from Sofaia, *ca.* 400 meters. Intergradation with the southern leeward coast form, *girafus,* is extensive and has caused the greatest confusion possible. This has been true because both are spotted forms, and the zone of intergradation includes both the towns of Basse-Terre (MCZ 71231-44) and Ste. Claude (MCZ 71287-303) — the two largest settlements on the island of La Guadeloupe. Evidence of *alliaceus* influence is present at sea level east of Basse Terre: MCZ 71223-48, from Delgres, and MCZ 71245-58, from Vieux Fort are intermediate series. This interesting region, where montane influence extends right to the coast, will be considered under "Evolutionary Discussion." Typically, the intermediates show a pattern closely approaching *alliaceus* and coloration similar to *girafus*. Underwood's description of BMNH 1946.8.28.96, the holotype, does not rule out the possibility that this specimen may have come from this intermediate, southern tip population. Assignment of the name *alliaceus* to the montane form is, therefore, arbitrary, but supported by the described resemblance of the holotype's pattern to that of the montane form (the holotype's coloration in life is, of course, not available for discussion). In reality, these two forms are not confusingly similar, even in preservative, but very careful attention must be paid to their diagnostic characteristics if confusion, due to the spotted pattern generally present in both, is to be avoided. This is an example of a case where obvious, bold markings can be more confusing than useful simply because they are variably present in both forms, whereas more subtle characters can always be relied upon to be consistent and definitive.

ANOLIS MARMORATUS GIRAFUS[1] subsp. nov.

Holotype: MCZ 71259, collected 14 August 1961 by J. D. Lazell, Jr.

Type locality: Vieux Habitants, La Guadeloupe.

Diagnosis: Dorsals in the standard distance 38 to 53 (average 47); 25 to 30 (average 28) subdigital lamellae; adult male blue-green to brown, always browner on the head and neck and always at least bluish on the posterior body and tail base; pale streaks and stipples, usually running together to form stripes that produce a reticulate pattern isolating dark spots, on the lateral trunk; throat fan pumpkin yellow with cream-colored to white scales. Adult female pale grey-brown with broken middorsal pattern.

Description of holotype: This adult male was warm brown on the head and neck, somewhat mottled with darker grey-brown. Posteriorly the ground color was pale blue-green, becoming bluer on the base of the tail. On the sides of the neck, in the axillary region, and along the lower costal region were dark grey-brown, polygonal spots separated by a pattern of broad, pale, cream to bluish reticulations which blended with the posterior ground color. The belly was dirty white. The throat fan was bright pumpkin yellow with white scales. (See Figure 8.)

---

[1] The name *girafus* has been invented to indicate the reticulate pattern.

Variation: This is the most variable form on La Guadeloupe. As with *A. o. cabritensis* on Dominica (see Lazell, 1962, p. 470), there is some correlation of variation and geography. In the southern part of the range specimens are often quite bright blue-green and have a well developed pattern of reticulations that sometimes leave only a few, well-isolated dark dots in the axillary region. In the northern part of the range many specimens have merely several series of light spots along the sides which, though they coalesce, fail to produce a very reticulated pattern; northern specimens are also rather bright greenish. In the central portion of the range there is a dilution of green to the point where often only a faint blue tinge remains on the posterior body and tail base of an otherwise dingy grey-brown anole; too, in the central part of the range, the entire animal may be so dingy that the light spots and reticulations only show up in strong contrast when the animal is in the dark phase. There are no sharp breaks in this variation, and, in fact, specimens that approach all of the described variations can be collected in any part of the range. Therefore, though there are average differences in color pattern, the clinality and inconsistency of this variation precludes dividing this form up into a number of races with smaller ranges. All specimens from all parts of the range fit the diagnosis given for the subspecies. Some pattern variants are shown in Figure 8.

The adult females vary from fawn-brown to ash-grey, and have a paler middorsal stripe set off by coalescing dark spots. This produces what I have called the ''broken'' middorsal pattern.

Distribution: A. m. girafus occurs along the leeward coast of La Guadeloupe from just northwest of Basse-Terre to Malendure. This is the driest region on La Guadeloupe, and perhaps in the entire archipelago. It corresponds, as has been pointed out, with the northern leeward coast of Dominica. Convergence between the anoles occupying these two areas will be considered under ''Evolutionary Discussion.''

Paratypes: MCZ 71260-77, same data as the type; MCZ 71278-86, Baillif; MCZ 71304-18, Marigot; MCZ 71319-28, Boulliante; MCZ 71329-37, Malendure.

Discussion: Intergradation with *alliaceus* has been discussed under that form. *A. m. girafus* also intergrades with the north

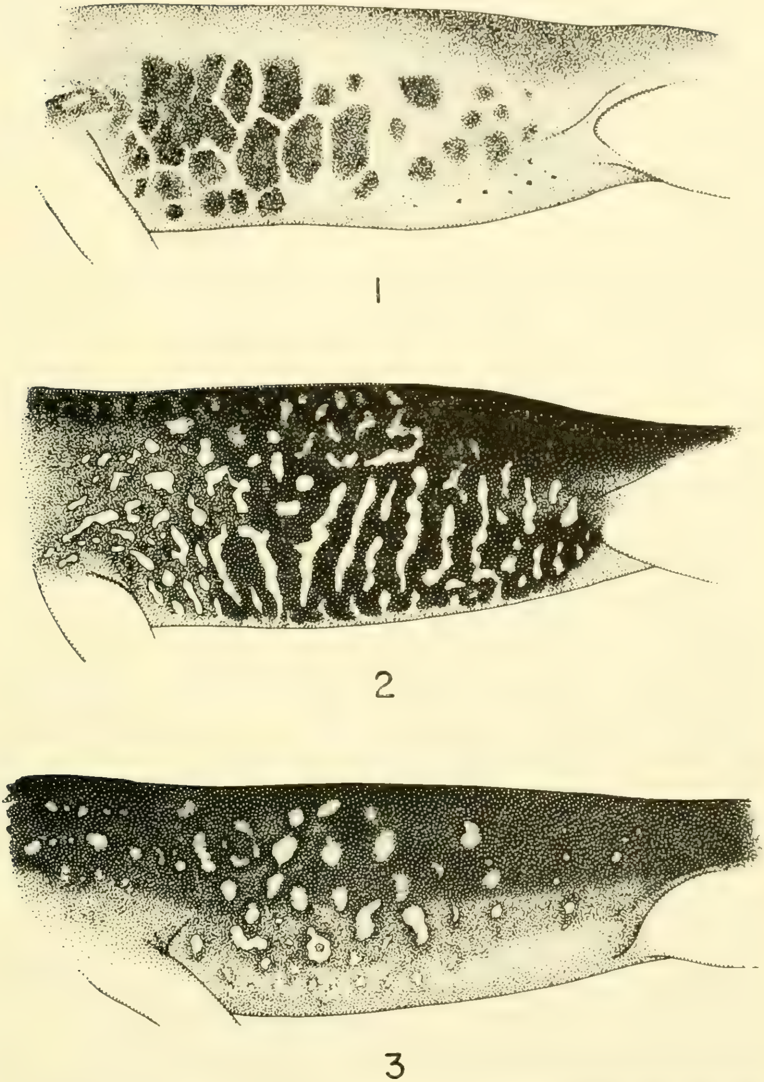


Figure 8. Pattern variation in adult male *Anolis marmoratus girafus*: 1. MCZ 71529, the type; 2. MCZ 71331; 3. MCZ 71304.

coast form, *setosus*, at the following localities: Anse Caraibe: MCZ 70850-58; Pointe Noire: MCZ 70841-49; Trou-Caverne: MCZ 70859-68; Ferry: MCZ 70869-82. These intergrades tend to extremes: from any one locality within the zone of intergradation one may collect specimens that closely resemble either *girafus* or *setosus*, though the majority show a variable combination of characteristics.

ANOLIS MARMORATUS SETOSUS[1] subsp. nov.

Holotype: MCZ 70813, collected 11 August 1961 by J. D. Lazell, Jr.

Type locality: Pointe Allègre, La Guadeloupe.

Diagnosis: Dorsals in the standard distance 38 to 53 (average 47); 22 to 28 (average 25) subdigital lamellae; dorsal scales spinose, those of the nape region so much taller than broad that a distinctly furred effect is produced; adult male blue-green with sooty transverse markings and a dark stripe through eye indicated when changing to the dark phase; throat fan yellow with greenish scales; belly pale, but without yellow tint. Adult female without a middorsal pattern as such, but with a variegation of green, brown, slate, and white speckles and blotches on dorsum, and bold, dark streaks on the lateral venter.

Description of holotype: This adult male was a nondescript green lizard immediately distinctive only because of the most peculiar character of the squamation. The dorsal ground color was green, shading to blue-green posteriorly and with some bluish wash on the head. The sooty transverse markings were not apparent except when changing from the light to the dark phase, or *vice versa*. The stripe through the eye was, however, noticeable in any phase. The belly was pale green; the throat fan was bright yellow with greenish or grey-green scales. Color change was to much darker, rendering the specimen almost black dorsally, and obliterating the dorsal markings — which, though diagnostic, seem to be never more than temporary. The type had several clusters of one to six bright yellow scales on the neck in no particular arrangement. The squamation is the most distinctive feature. It is, nevertheless, difficult to describe. The dorsals are conical to the point of being spines; this condition is accentuated in the nape region, and quite literally gives the most furred effect imaginable on an anole (see Figure 9). The holotype, the largest specimen examined, measured 66 mm snout to vent.

---

[1] *Setosus*, Latin, for "bristly."

Variation: The diagnostic color pattern and squamation are quite consistent, but the amount of blue varies from the condition described for the holotype to a general blue wash. The peculiar clusters of yellow "spines" (scales) on the neck appear only in occasional adult males and are not relevant to the taxon.

The adult female is variable but always variegated and lacks a genuine middorsal pattern. The ground color is blotchy green, and brown, slate-grey, and pale grey or white mottles and blotches are present. There are bold, dark series of stipples forming streaks along the sides of the otherwise dirty white venter.

Distribution: This form is confined to the northern coast of La Guadeloupe.

Paratypes: MCZ 70814-19, same data as the type; MCZ 10403-27, Ste. Rose (Noble coll.); MCZ 70804-12, Ste. Rose; MCZ 70820-32, Deshaies; MCZ 70833-40, Rifflet.

Discussion: It was specimens of this form, plus intergrades between *alliaceus* (*sensu* Lazell) and *girafus*, that constituted Underwood's concept of *alliaceus*. As Underwood noted, Williams regarded the Ste. Rose series as distinct. Williams (pers. comm.) was on the verge of describing the Ste. Rose series as a distinct species because of the remarkable squamation when the first shipment of my anoles from the Guadeloupe region arrived; this shipment contained intergrades between *setosus* and *speciosus*, as well as the other two forms *setosus* touches on. Credit for its most apt and descriptive name, however, remains with Ernest E. Williams.

Intergradation with *alliaceus* and *girafus* has been discussed under those forms, respectively. Intergrades between *setosus* and *speciosus* occur along the extreme northeast coast of La Guadeloupe between Lamentin (MCZ 70988-96) and Morne Rouge (du Nord) (MCZ 70997-1003).

The population on Ilet-à-Fajou, intermediate generally between *setosus* and *speciosus*, requires discussion separately. MCZ 71004-13 from Ilet-à-Fajou fit the diagnostic color characters of *speciosus* (see diagnosis of that form) quite closely. I would have included them, therefore, under this form except that E. E. Williams pointed out the rather spinose character of their squamation. The combination of *setosus*-type squamation and *speciosus*-type coloration and pattern is common in mainland intergrades between these two forms, and it is quite plausible to speculate that the Ilet-à-Fajou population was derived from a few specimens, from the adjacent coast, which had this combination; this might explain its consistency in Ilet-à-Fajou anoles. A careful examination of these anoles, however, revealed another interesting fact: they possess rather large scales — there being only 33 to 43 (average 37) contained in the standard distance. Since the character is not diagnostic, it fails to differentiate this population as a taxon, but indicates that a trend towards abnormally large scales may be expected in *Anolis marmoratus* populations confined to very small islands. I have tentatively assumed that this characteristic can, in fact, be expected, and on that entirely shaky foundation classify the following form as:

ANOLIS MARMORATUS KAHOUANNENSIS subsp. nov.

Holotype: MCZ 70791, collected 28 August 1961 by J. D. Lazell, Jr.

Type locality: Ilet-à-Kahouanne, Guadeloupe Passage, NW of La Guadeloupe.

Diagnosis: Dorsals in the standard distance 30 to 38 (average 33); 22 to 28 (average 25) subdigital lamellae; dorsal scales conical, producing a bulldog-collar-spike effect on the nape; adult male chartreuse (= bright yellow-green) with no markings except bluish washes on the head and chin; belly bright yellow; throat fan bright yellow with yellow scales. Adult female chartreuse with a bright yellow belly and no markings except occasional traces of a ladder middorsal pattern.

Description of holotype: In my field catalogue I have described this adult male as "a solid, brilliant chartreuse anole. Changes to dark green but never has any markings." There was a bluish wash on the snout and temporal region which continued onto the chin and anterior edge of the throat fan. The throat fan was pumpkin-yellow with bright yellow scales. The belly was butter-yellow. The orbital region was pale. Color change, as noted, was merely to darker. The scales are extremely large, and the difference between them and the scales of mainland anoles may be readily noticed in the field. Combined with their large size is the *setosus*-like characteristic of spinosity (though not to nearly so great an extent); the effect of conical, spike-like dorsal scales, especially on the nape, is striking (see Figure 9). The holotype, the largest specimen examined, measured 76 mm snout to vent.

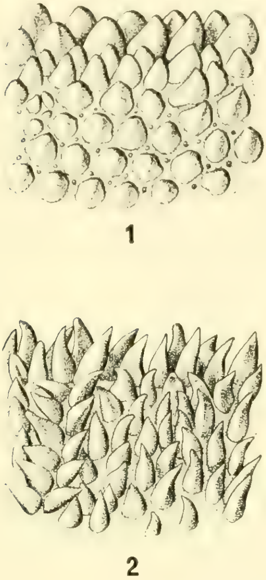


Figure 9. Nape scales just lateral to the dorsal midline in two forms of *Anolis marmoratus:* 1. *kahouannensis,* type (MCZ 70791); 2. *setosus,* type (MCZ 70813).

Variation: The extent of blue wash on the heads of males varies from the condition described for the holotype to virtually absent. One specimen (MCZ 70792) darkened in blotches when changing to the dark phase; this was only vaguely reminiscent of the condition visible in *setosus.*

The adult female is almost completely without markings. There is no mottling, stippling, or streaking, though occasional segments of the ladder middorsal pattern characteristic of the young female may be retained in sexually mature individuals. The basic color is pea-green, and the belly is bright yellow.

Distribution: This anole is confined to Ilet-à-Kahouanne.

Paratypes: MCZ 70792-803, same data as the type.

Discussion: Assignment to subspecific rank under *marmoratus* is, in this case, an arbitrary action supported only by direct evidence, in the Ilet-à-Fajou population, that a tendency towards large scale size *can* occur in small, isolated *marmoratus* populations. Because the Ilet-à-Fajou population does demonstrate that enlarged scale size is within the potential evolutionary role of *marmoratus*, it is at least possible to regard *kahouannensis* as a subspecies of *marmoratus* with respect to this character.

It is, however, disquieting to note that *kahouannensis* is 100 per cent distinct on the basis of coloration in life, quite apart from the scale size discrepancy. In the final analysis, there is no conclusive argument for the inclusion of this form within the *marmoratus* species; there is, nevertheless, a tenable argument that it should be included, since all of the mainland Guadeloupéen forms are 100 per cent distinct on the basis of coloration in life if intergrades are not considered. *A. m. kahouannensis* has no possibility of producing an intermediate population with the mainland forms, but I have, nevertheless, accepted it as a subspecies of *marmoratus* because such a judgment is tenable and because in my own opinion *kahouannensis* is not more distantly related to *setosus* than *setosus* is to those mainland forms with which it intergrades directly. My opinion is based on a general impression of these taxa both in life and after preservation; it is thus the sort of opinion that can neither be proven nor disproven on the basis of present information. Authors who wish to regard this form as a species distinct from *marmoratus* can find ample justification for doing so. However, the Kahouanne Island anole resembles *setosus* with regard to the convexity and spinosity of the dorsal scales, and fits *A. marmoratus* generally with regard to the prenasal and the ventral keeling.

ANOLIS MARMORATUS SPECIOSUS Garman

Anolis speciosus Garman, 1887, Bull. Essex Inst., 19:45. Cotypes: MCZ 6172, 70947-50.

Lectotype: Here designated as MCZ 6172, collected by Richardson, March, 1886.

Type locality: "Marie Galante" (in error); here revised to Pointe-à-Pitre, Grande Terre.

Diagnosis: Dorsals in the standard distance 32 to 50 (average 40); 20 to 26 (average 23) subdigital lamellae; adult male green, without dorsal markings; venter brightly washed with yellow; orbital area sky-blue; throat fan sulfur-yellow with greenish scales. Adult female olive with ladder or striped middorsal pattern.

Description: MCZ 70961, an adult male from Pointe-à-Pitre, in life was bright green over the entirely unmarked dorsum.

The venter was entirely washed with bright yellow, producing a deep yellow-green zone along the sides. The orbital skin was sky-blue, and sharply set off from the green color of the rest of the head. The throat fan was sulfur-yellow with green-grey scales. This male had several clusters of yellow scales scattered on the sides of the neck, reminiscent of some *setosus* males. The scales of the dorsum are not spinose (i.e. never taller than broad), and closely resemble the dorsal scales of anoles (excluding *setosus*) from La Guadeloupe. Color change involved merely a darkening of the ground color to slatey-green, accompanied by greying of the orbital skin. This specimen, the largest examined, measured 71 mm in snout-vent length.

The adult female is olive-green, has a striped or ladder mid-dorsal pattern, and lacks other distinctive markings including a flank stripe.

Variation: This form is remarkably constant in color characters. As with *setosus,* the presence of yellow scale clusters on the neck is occasional in old adult males and not relevant to the taxon. Specimens from Ilet-à-Cochons and the south coast of Grande Terre sometimes show a more gradual blending of the blue coloration of the orbital region with the green of the head than do specimens from the more northern portions of the range. There is, however, never a dark stripe through the eye, as in *setosus.*

Distribution: This form occurs throughout SW Grande Terre (i.e., the wetter area of this island), on the "waist" between Grande Terre and La Guadeloupe, and on Ilet-à-Cochons (sometimes called, uncomplimentarily enough, Ilet-à-Gouvernement).

Specimens examined: MCZ 6172, "Marie Galante," Lectotype (Richardson coll.); MCZ 70947-50, "Marie Galante," Paralectotypes (Richardson coll.); MCZ 70913-24, Abymes; MCZ 70925-34, Gosier; MCZ 70935-46, Ste. Anne; MCZ 70951-60, Baie Mahault; MCZ 70961-77, Pointe-à-Pitre; MCZ 70978-87, Ilet-à-Cochons, ou Gouvernement.

Discussion: The locality of this form given by Garman (presumably *fide* Richardson) in the original description is incorrect. The five males in the type series (MCZ 6172, 70947-50) fit quite precisely with the form from SW Grande Terre on squamation characters and are powder-blue from long preservation. They completely lack markings such as the faint flank stripe and brown head (which does not turn blue in preservative) that characterize the NE Grande Terre population, the only other form that these long-preserved specimens might conceivably be confused with. Richardson demonstrably collected in both Désirade and Marie Galante. It would have been remarkable indeed if he had failed to stop at the large and busy port of Pointe-à-Pitre while in this area. To add to the evidence against the "Marie Galante" locality is the fact that no specimen resembling *speciosus* has ever been collected there since, whereas the Marie Galante anole, *ferreus,* is common indeed — though its original type locality was cited as "Guadeloupe."

Intergradation with nominate *marmoratus, alliaceus,* and *setosus* has been discussed under those forms, respectively. Intergradation with the dry country form of NE Grande Terre, *inornatus,* occurs along a line through Morne-a-L'Eau (MCZ 70885-94), Chateau Gaillard (MCZ 70895-902), and St. François (MCZ 70903-12).

ANOLIS MARMORATUS INORNATUS[1] subsp. nov.

Holotype: MCZ 71036, collected 13 August 1961, by J. D. Lazell, Jr.

Type locality: Anse Bertrand, Grande Terre.

Diagnosis: Dorsals in the standard distance 38 to 53 (average 47); 20 to 26 (average 25) subdigital lamellae; adult male pale grey-green on trunk, rich brown on head; orbital area brown; belly pale lime-green; throat fan yellow with white to cream-colored scales; flank stripe indicated. Adult female pale grey-brown with striped middorsal pattern and flank stripe.

Description of holotype: This adult male was pale green with a bluish tinge on the posterior body and tail base. The head was warm brown; the orbital skin golden brown. The brown of the head graded gradually into the green of the dorsum. There were faint, grey-brown vermiculations on the nape. The belly was pale, dirty green posteriorly, becoming lime-green in the chest region. The throat fan was dull yellow with white scales. A flank stripe, paler grey-green than the dorsal ground color, extended from the shoulder to the hind limb insertion. There were faint indications of darker grey-brown transverse markings across the dorsum. The slight color change involved a general trend towards becoming darker and browner. This specimen, the largest examined, measured 75 mm snout to vent.

Variation: This form is rather variable. Some specimens lack all signs of neck vermiculations or transverse markings. The amount of green varies from the condition described for the holotype to one in which it is virtually restricted to the posterior belly and rump regions. In most specimens the throat fan appears to have a paler yellow border and a brighter yellow center, and the scales of the fan are often closer to cream-color than white. The variation is individual and does not correspond to different localities within the range of the form.

---

[1] *Inornatus,* Latin, for "unadorned."

The adult female is pale tan to ash-grey on the dorsum, and always brownish on the head. The striped middorsal pattern is not bold but is always noticeable. A definite flank stripe is indicated in the thoracic region.

Distribution: This form occurs throughout northern Grande Terre and extends southeastward along the northeast coast of that island towards, but not to, Pointe-des-Chateaux.

Paratypes: MCZ 71037-42, same data as the type; MCZ 61082-92, Moule (Proctor coll.); MCZ 71014-19, Moule; MCZ 71020-25, Petite Canal; MCZ 71026-35, Port Louis; MCZ 71043-48, Campeche; MCZ 71049-57, town of Ste. Marguerite.

Discussion: Intergradation with *speciosus* has been discussed under that form. The population on the Pointe-des-Chateaux peninsula requires especial consideration. The males from this area show definite vermiculation on the nape, and usually a few bold, dark spots at least in the dark phase. There is a noticeable yellow wash along the sides and the orbital skin has a distinctly orangish tone in some specimens. In keeping with the norm of intergrade populations in the archipelago, these anoles are very variable: some closely resemble *inornatus* in important respects, others closely approach the anole found on the adjacent island of La Désirade. Therefore, MCZ 71058-67, from Pointe-des-Chateaux, are regarded as a sample of an intermediate population between *inornatus* and the following form:

ANOLIS MARMORATUS DESIRADEI subsp. nov.

Holotype: MCZ 71068, collected 14 September 1961, by J. D. Lazell, Jr.

Type locality: Grande Anse, La Désirade.

Diagnosis: Dorsals in the standard distance 32 to 50 (average 40); 22 to 28 (average 25) subdigital lamellae; adult male pale greenish with yellow wash on sides and yellow belly; dorsal surfaces extensively vermiculated with darker grey-brown; throat fan yellow with white to cream-colored scales; orbital area bright rust-red; chin yellow with bold blue-grey streaking. Adult female grey-greenish with grey head and yellow belly; middorsal pattern obsolete.

Description of holotype: This adult male was pale grey-green boldly vermiculated with dark grey-brown all over the dorsal surfaces of the trunk and legs. The lateral surfaces were washed with yellow, and the belly was bright yellow. A lack of vermiculation along the side indicated a vague flank stripe. The chin was yellow and blue-grey bars ran from the anterior base of the throat fan to the infralabials. The head was dull brown to grey-brown, and the bright rust-red of the orbital skin stood out in bold contrast. The throat fan was yellow with cream-colored scales. Color change involved general darkening and increased brownness; the vermiculations became especially bold in the dark phase. The holotype, the largest specimen examined, measured 80 mm snout to vent.

Variation: There is a definite cline in extent of yellow on the sides and in the ground color, increasing as one proceeds eastward along La Désirade. Some specimens from all over the island show small orangish patches on the nape and anterior body; this is by no means constant and not characteristic of the taxon.

The adult female is distinctly grey on the head and becomes greener posteriorly. There is no indication of vermiculation. The belly is distinctly yellow. Young specimens show a vague striped middorsal pattern, but those apparently mature females were somber grey middorsally, producing the pattern I have called obsolete.

Distribution: This form is confined to the island of La Désirade.

Paratypes: MCZ 57285-96, "Desirade Id." (Richardson coll.); MCZ 62210-1, Ravine la Rivière (Proctor coll.); MCZ 62212, Le Calvaire (Proctor coll.); MCZ 62213-17, Grande Anse (Proctor coll.); MCZ 71069-77, Grande Anse; MCZ 71078-87, Pointe-des-Colibris; MCZ 71088-100, Le Souffleur; MCZ 71101-12, Pointe Double.

Discussion: The intermediate population between *inornatus* and *desiradei* has been discussed under that form. It need only be pointed out here that this population, while not one of "intergrades" as such, precludes the possibility of recognizing *desiradei* as a species distinct from *marmoratus:* on Pointe-des-Chateaux, Grande Terre, some anoles that are unequivocally *marmoratus* show *desiradei* characteristics.

Beginning with *desiradei* there is a stepped-cline series through the "satellite" islands of the archipelago. The first population of this series is:

ANOLIS MARMORATUS CHRYSOPS[1] subsp. nov.

Holotype: MCZ 70649, collected 4 September 1961, by J. D. Lazell, Jr.

Type locality: Terre de Haut, Les Iles de la Petite Terre.

Diagnosis: Dorsals in the standard distance 30 to 42 (average 36); 22 to 28 (average 25) subdigital lamellae; adult male somber green-grey with bright yellow suffusion on the sides and bright yellow belly; vermiculations present on the anterior trunk and nape, at least, and dark dotting usually present on remaining dorsal surfaces; orbital area red-gold; chin entirely blue-grey; throat fan yellow with pale yellow scales. Adult female grey with yellow belly, an obscure striped middorsal pattern, and a brief flank stripe.

Description of holotype: This adult male was grey-green, becoming greener posteriorly and virtually grey (or grey-brown) on the head. The yellow of the venter extended as a bright suffusion over the lateral trunk. The vermiculations tended to break up into small speckles on the posterior body and hind limbs; no notable lack of vermiculation distinguished a flank stripe region. The chin was entirely blue-grey, and the skin of the orbital area was red-gold. Color change was merely to slightly darker and browner. The holotype, the largest specimen examined, measured 73 mm snout to vent.

Variation: The extent of vermiculation and its break-up into speckling is rather variable, but specimens always show vermiculation as such at least on the nape and anterior trunk. Some specimens showed a vague indication of the vermiculation-free flank stripe area, though this region is usually heavily invaded with yellow. The color of the orbital skin and the uniformity of the blue-grey chin are constant features.

The adult female is distinctly duller and greyer than the average *desiradei* female and retains the striped middorsal pattern. The contrast between the grey of the head and the green-grey of the dorsum is not marked, though the belly is bright yellow. A short flank stripe is present.

Distribution: Terre de Haut and Terre de Bas, Les Iles de la Petite Terre.

---

[1] *Chrysos*, Latin, for "gold," plus *ops*, Greek, for "appearance."

Paratypes: MCZ 70656-65, same data as the type; MCZ 70650-5, Trou Canard, Terre de Bas, Les Iles de la Petite Terre.

Discussion: The Petite Terre anole agrees with *desiradei* in possessing vermiculations, though they are reduced from the condition in that form; it agrees, on the other hand, with *ferreus* in having a uniform blue-grey chin, though the blue-grey does not extend onto the throat fan, as it usually does in *ferreus.* The orbital skin color, though entirely distinctive, is what one would expect of a mixture between the rust-red of *desiradei* and the dull yellow of *ferreus.* The extent of yellow on the lateral surfaces is likewise intermediate between these two forms. Dorsal scale size shows a marked overlap with *desiradei,* on the one hand, and *ferreus,* on the other. Some adult males have the neural spines of the caudal vertebrae distinctly more elongate than in any *desiradei* and as elongate as in some *ferreus.* Therefore, in every respect except maximum snout-vent length (in the sample available), *chrysops* is morphologically intermediate between two extremes: *desiradei* and *ferreus.*

In contrast with the Ilet-à-Fajou population, which is also an isolated morphological intermediate, *chrysops* is entirely distinctive in its own right; there is no intergrade population with which *chrysops* individuals could be confused, and there are diagnostic characteristics by which *chrysops* may be unequivocally distinguished. For these reasons *A. m. chrysops* is granted nomenclatural rank. Because it is an intermediate population between *A. m. desiradei* and *ferreus* of Marie Galante and because it is geographically intermediate as well, it connects the Marie Galante anole with the remainder of the *marmoratus* series, and *ferreus* must therefore be regarded not as a distinct species but as:

ANOLIS MARMORATUS FERREUS (Cope)

Xiphosurus ferreus Cope, 1864, Proc. Acad. Nat. Sci. Philadelphia, 168. Type: BMNH 1946. 8.5.59., no collector, no date.

Anolis asper Garman, 1887, Proc. Essex Inst., 19: 31. Syntypes: MCZ 6162. (Type locality Marie Galante.)

Type locality: "Guadeloupe" (in error); here revised to Morne Constant, Marie Galante.

Diagnosis: Dorsals in the standard distance 22 to 33 (average 28); 25 to 30 (average 28) subdigital lamellae; adult male somber grey-brown becoming greener posteriorly; dorsum sprinkled with dark dots seldom coalescing to form short vermiculations; suffusions, often forming blotches, of yellow laterally;

orbital area dull yellow; uniform blue-grey of chin often invading otherwise yellow throat fan with yellow scales. Adult female grey-brown to greenish with brief flank stripe, obsolete middorsal pattern, and a very pale yellowish belly.

Description: An adult male from Morne Constant was dingy grey-brown shading to brownish blue-green on the tail and dull blue-grey on the head. The sides were suffused with rich yellow, forming large blotches anteriorly. The venter was duller, paler yellow. The chin was entirely blue-grey, and this color invaded the anterior quarter of the throat fan; the remainder of the throat fan was bright yellow with yellow scales. The orbital region was dull yellow, strikingly distinct from the blue-grey of the snout, though less abruptly blending into the browner grey of the temporal region. The nape and dorsum were liberally speckled with dark grey-brown. This specimen, MCZ 70748, shows a remarkably high tail crest, and, in life, had three to five longitudinal chestnut-brown stripes along that crest. This specimen measured 99 mm snout to vent, though a specimen from Vieux Fort (the largest examined), MCZ 70767, measured 119 mm snout to vent, thus 21 mm larger than the largest *ferreus* previously recorded (Underwood, 1959, p. 203).

The adult female is usually much greener than *chrysops* and always lacks the brightness of the yellow belly. Large specimens have the striped middorsal pattern reduced to obsolescence: a short flank stripe, in the shoulder region, is noticeable.

Variation: The speckling ranges from the condition described above to but a few scattered stipples, covering one to four scales, in the nape region: thus, from nearly the condition of *chrysops* to nearly the condition of *terraealtae* (which completely lacks speckling or stipples). The extent of yellow suffusion and the presence of yellow blotches on the anterior trunk actually varies from the condition of *chrysops* to that of *terraealtae*, and is less distinctive. The height of the caudal crest, even in old males, is extremely variable and cannot be used to delimit the taxon; likewise, the presence of longitudinal streaking along the tail crest is merely an occasional character and not relevant to the taxon. Throat fan coloration varies tremendously; the condition described for MCZ 70748 is very common, but the fan may be entirely yellow without blue-grey invasion, sharply divided in half between the two colors, or largely grey with yellow reduced to the posterior portion. One specimen, MCZ 70769, had an entirely blue-grey throat fan. In view of my experience with *ferreus* in the field, Barbour's description of the throat fan as grey with a wide lemon yellow margin (Underwood, 1959, p. 203) is puzzling. It is suggested that Barbour added this note as an afterthought, based on a combined recollection of some *ferreus* with bicolored fans and the fact that other anoles with bicolored fans often have an arrangement of center-color contrasted to margin-color.

Females are likewise variable; young specimens look very much like the female anole from Terre de Bas, Les Iles des Saintes, though they would show an absolute scale size discrepancy with that form. Older specimens are notably darker and often greener than females of adjacent populations and often show a definite bluish tinge.

Distribution: This form is confined to the island of Marie Galante.

Specimens examined: MCZ 6162 (17), "Marie Galante" (Richardson coll.); MCZ 28526-50, "Marie Galante" (Barbour coll.); MCZ 61093-95, 62218-27, St. Louis (Proctor coll.); MCZ 62228, Les Sources (Proctor coll.); MCZ 70748-58, Morne Constant; MCZ 70759-61, Capesterre; MCZ 70762-66, Grand Bourg; MCZ 70767-71, Vieux Fort; MCZ 70772-78, Ste. Germaine; MCZ 70779-84, Grelin; MCZ 70785-90, Pointe-des-Basses.

Discussion: Anolis marmoratus ferreus is the end of a cline in scale size and extent of blue-grey chin pigment that begins on Désirade; with respect to the extent of yellow on the lateral surfaces and dorsal marking it is intermediate between *chrysops* and the form next to be discussed, *terraealtae*. As with *chrysops*, *terraealtae* overlaps *ferreus* broadly in scale size, and even somewhat in the height of the neural spines on the caudal vertebrae. With respect to some characters, then, *terraealtae* is the continuation of the cline southwestward from Désirade; with respect to most of its other characters it is intermediate between *ferreus* and the final population of *marmoratus: caryae* of Terre de Bas, Les Iles des Saintes.

ANOLIS MARMORATUS TERRAEALTAE Barbour

Anolis terraealtae Barbour, 1915, Proc. Biol. Soc. Washington, 28: 76. Type: MCZ 10627, collected by Noble, no date.

Type locality: "Terre d'en Haut, Iles des Saintes"; here restricted to Pompiere, Terre de Haut, Les Iles des Saintes.

Diagnosis: Dorsals in the standard distance 28 to 40 (average 33); 20 to 26 (average 25) subdigital lamellae; adult male grey-brown to green-brown, without dark speckles or vermiculations; large blotches of bright yellow laterally and on nape fading to suffusions on posterior body and belly; yellow of orbital area often confluent with yellow blotching of nape and trunk; throat-fan yellow with yellow scales. Adult female grey-brown with a faint flank stripe briefly indicated and a striped or ladder middorsal pattern.

Description: An adult male from Pompiere, MCZ 70707, was pale brown-green, becoming browner on the head and blue-green on the tail. The orbital skin was ochre-yellow and suffused into the brown of the head. Virtually the entire costal region and lateral nape was blotched with three or four large areas of bright yellow pigment. There was no trace of dark marking. The throat fan was orange-yellow with yellow scales. The venter anteriorly was pale blue-green, almost lime-green, and faded to yellow in the abdominal region. Color change was merely to somewhat darker and browner. This specimen measured 76 mm snout to vent; a larger specimen, MCZ 70687, from Pointe Basse, Grande Ilet, measured 80 mm snout to vent and is the largest examined.

The adult female is pale grey-brown with a distinctly striped middorsal pattern. There is a short flank stripe, but it is not set off by darker borders above or below.

Variation: Throat fan color varies from butter-yellow to orange-yellow, and the scales vary from pale to bright yellow. Some specimens show rather heavy yellow pigmentation of the entire venter. Females vary little, and no geographic variation was noted in either sex among the several islands where this form occurs.

Distribution: A. m. terraealtae occurs throughout the low, dry area of Les Iles des Saintes; this includes Ilet-à-Cabrit, eastern Terre de Haut, Grande Ilet, and, presumably, La Coche. This area forms a crescent around the high, wetter, western end of the island of Terre de Haut and lies to the east of the also high, wetter island of Terre de Bas.

Specimens examined: MCZ 10628-30, "Terre d'en Haut" (Noble coll.); MCZ 70687-96, Pointe Basse, Grande Ilet; MCZ 70697-706, Ilet-à-Cabrit; MCZ 70707-17, Pompiere, Terre de Haut; MCZ 70718-22, Marigot, Terre de Haut.

Discussion: The type locality is restricted to Pompiere because the population on the western end of the island of Terre de Haut is intermediate between *terraealtae* and the form which occurs on Terre de Bas, *caryae*. Of fifteen specimens collected in the town of Terre de Haut (MCZ 70723-37), three (70730-32) show definite *caryae* characteristics of both coloration and, to a slight extent, squamation. Several others of this series show an approach to *caryae* on squamation. An additional series, MCZ 70738-47, from Pointe-à-Cointe, Terre de Haut, are quite intermediate in squamation and vary considerably in color characters, approaching both *terraealtae* and *caryae*. The type series is severely discolored; on the basis of scale characters alone, however, they fit within the range of the form which occurs in the low, dry "crescent" of Les Saintes. These specimens probably were collected in the town of Terre de Haut, but on the basis of what can be discerned from them the name must, ironically, be applied to the form which occurs on the eastern end of the island of Terre de Haut. There is no precise locality data with them that could contradict restriction of the type locality to Pompiere. As in the case of the Pointe-des-Chateaux population between *inornatus* and *desiradei*, the population on western Terre de Haut is not of intergrades as such, but it is one which is both morphologically and geographically intermediate between two very different forms and not distinctive in its own right. The presence of this intermediate population necessitates classifying the last form to be described as:

ANOLIS MARMORATUS CARYAE subsp. nov.

Holotype: MCZ 70666, collected 6 September 1961 by J. D. Lazell, Jr.

Type locality: The town of Terre de Bas, Terre de Bas, Les Iles des Saintes.

Diagnosis: Dorsals in the standard distance 38 to 53 (average 47); 20 to 26 (average 23) subdigital lamellae; adult male pale green, becoming bright green posteriorly; a faint wash of yellow on abdomen, rest of belly lime green; fine vermiculations coalesce on the back of the head and the nape to produce a grey appearance; posteriorly these fine vermiculations produce distinct pale grey transverse markings; a pale, whitish flank stripe accentuated in the costal region by a lack of vermiculation; throat fan bright yellow with yellow scales; orbital area cream-colored. Adult female pale grey-green with ladder middorsal pattern and striking flank stripe set off by dark speckles above and below.

Description of holotype: This adult male was pale green with fine vermiculations so pronounced on the head, neck and anterior dorsum that the ground color appeared only as flecking in this area. There was a sharp transition between this vermiculation and the grey transverse bands, though neither the vermiculations nor the bands were dark or bold compared to the green ground color. The flank stripe appeared as a continuation of the pale whitish chin and throat color and extended beyond the first transverse band. The throat fan was bright yellow with yellow scales, and the orbital skin was cream-colored. The dorsal scales are very small though not spinose. Color change was negligible. The holotype, 75 mm snout to vent, was the largest specimen examined.

Variation: The orbital skin may be pale yellow or cream-colored, probably depending more on the eye of the observer than anything else. Variation in this population is so slight with respect to the known sample that it defies description.

Distribution: This form is confined to Terre de Bas, Les Iles des Saintes.

Paratypes: MCZ 70667-76, same data as the type; MCZ 70677-86, Grande Anse, Terre de Bas, Les Iles des Saintes.

Discussion: That two such different anoles occur in the Saintes came as a complete surprise. When I discovered this fact I was struck by the similarity of *caryae* to *chrysops*, for I had not yet seen *desiradei*. In general, *caryae* bears a reremarkable resemblance to a pale, faded *desiradei*, though there is, of course, an ample set of characters to unequivocally distinguish them. It is suggested that, aside from parts of the large and ecologically variable island of Marie Galante (see "Evolutionary Discussion"), the islands of Désirade and Terre de Bas are more ecologically similar than any of the other "satellite" islands: both are fairly high and rather homogeneously wetter than any other islands in the "satellite" group, including Marie Galante. The similarity between the anoles of Désirade and Terre de Bas, Les Saintes, is in my opinion the product of parallelism. There is no apparent resemblance between *caryae* and the anoles of La Guadeloupe except in those characters which define the species *marmoratus*. The relationships of *caryae* are obviously and directly to *terraealtae*, thence back through the stepped-cline series to *desiradei*, which is related to *inornatus* in the same manner as *caryae* is to *terraealtae*.

This form is named for Margaret M. Cary, who, in 1957, sponsored my first trip to the Caribbean; without her continuous inspiration and friendship since that time my life might have been a very different one, and I might never have seen the island of Terre de Bas.

EVOLUTIONARY DISCUSSION

The fact that geographic variation within a single species has produced so many geographic units, herein described as subspecies, is remarkable. As I noted for *Anolis oculatus* on Dominica, ecological zonation appears to have produced this situation. On Dominica there are four subspecies: nominate *oculatus*, on the south coast, *winstoni*, on the wet, windward coast, *cabritensis*, on the dry, northern leeward coast, and *montanus*, in the central rain forest.

Dominica is the largest and highest of the first cycle islands on which an *Anolis* of the *bimaculatus* group occurs; though somewhat smaller in area, La Guadeloupe is closely similar in topographical conformation, and a comparison of these two islands is called for with respect to their *Anolis*.

Ecological zonation is produced, among the first cycle islands of the Lesser Antilles, by a combination of two factors: the predominant northeast wind and a range of high mountains. The predominant northeast wind may be considered as a vector in which the eastern component is the result of the inertia of the air mass surrounding the rotating earth, and the northern component is the result of convection currents produced by warmed air rising from the equatorial regions, cooling in the upper atmosphere, descending at the poles and pushing across the surface of the earth towards the equator. (In the Northern Hemisphere this amounts to a northerly wind direction.)

The mountain factor of this etiological combination is more complex. Cumulus, produced directly by evaporation off the tropical Atlantic, can be backed up on a chain of mountains, providing they are high enough and sufficiently close together, in such a way as to produce both a rain (or "cloud") forest zone through the mountains themselves, and a well-watered lowland region to windward. The result of this to leeward of the mountains is a lowland zone of low rainfall and generally arid conditions. In Dominica a chain of mountains that are demonstrably high enough and sufficiently close together to act as a moisture barrier begins, in the south, with Morne Anglais, and extends northward to the massif of Morne Diablotin. The mountains increase in height from south to north, in this case, and the result is a larger rain forest area, and a correspondingly more arid leeward coast area, at the northern end of the island. There is a broad gap between the Morne Diablotin massif, however, and the smaller, lower Morne Au Diable massif at the north tip of the island. Morne Au Diable is, however, sufficiently high to back up cumulus of its own, and it also gets some rain from large amounts of cumulus backed up on Diablotin, at least during the rainy seasons of the year.

On La Guadeloupe a similar situation prevails: a series of peaks comparably high and continuous begins in the south with the Souffriere-Sans Toucher massif and continues northward to Morne Goton. There is not, however, a smaller, disjunct massif corresponding to Morne Au Diable in Dominica. Also, the highest montane area on La Guadeloupe is at the southern end: the Souffriere-Sans Toucher massif produces the largest rain forest area, and, correspondingly, the most arid region is the southern leeward coast. La Guadeloupe, then, has the ecological zonation of Dominica, but in mirror image.

On Dominica, the Morne Au Diable massif is well watered but never attains genuine rain forest conditions even at its highest points. The result of this is a large area at the north tip of Dominica that is a sort of "ecological mongrel." Rain forest, as such, does not appear, but the country is decidedly wetter at lower elevations than elsewhere on the island. This area contains an anole that is morphologically intermediate between a coastal form (*winstoni*) and the montane form (*montanus*), and this intermediate occurs at much lower elevations at the northern end of the island than do intergrades with *montanus* elsewhere.

On La Guadeloupe, where the Souffriere-Sans Toucher massif is at the south end, very close to the tip of the island, and there is no disjunct massif closer to the coast, the "ecologically mongrel" area is at the southern tip. It is therefore suggested that the presence of *alliaceus* influence at sea level, combined with coastal *girafus* influence, at the south tip of La Guadeloupe is directly the product of ecological conditions.

It may be noted, however, that in Dominica the tip-population anole is intermediate between the montane and *wet, windward coast* forms; on La Guadeloupe the tip-population is intermediate between the montane and *dry, leeward coast* forms.

Anolis oculatus montanus, of Dominica, is an entirely green anole with a dark throat fan and white, black-bordered, lateral spots. *Anolis marmoratus alliaceus*, of La Guadeloupe, is an entirely green anole with a dark throat fan and black, light-bordered, spots. The convergence is obvious, but I am unable to account for a selection pressure which would produce such spot-patterns.

Similarly, *Anolis oculatus cabritensis,* from the arid coast of Dominica, has a striped pattern composed of coalescing light spots on a darker ground color. *Anolis marmoratus girafus,* from the arid coast of La Guadeloupe, has pale, coalescing spot series. In this case the convergence seems to result from a selection pressure operating to produce ''outline-breaking'' color patterns in forms which occupy the sparsely vegetated scrub-thornbush areas of both islands. Similar ''outline-breaking'' patterns appear in most of the other dry country forms. There is also a correspondence between Dominica and La Guadeloupe dry country forms with respect to their clinality. In both cases a bright color begins at each end of the range and fades out clinally towards the middle.

A geographical convergence may be noted between the south coast form of *A. oculatus* (nominate *oculatus*), on Dominica, and the north coast form of *A. marmoratus* (*setosus*), on La Guadeloupe, but no morphological convergence is readily apparent.

La Guadeloupe has, in reality, two wet, windward coast forms: nominate *marmoratus* and *speciosus.* Southwestern Grande Terre is ecologically confluent with the ''waist'' between Grande Terre and La Guadeloupe (which is part of La Guadeloupe), and there is no reproductive break between *speciosus* on either side of the narrow estuary which separates them. In fact, though I never stopped to collect them, anoles were seen on the bridge across this estuary, Rivière Saline. There is no apparent morphological convergence between either of the La Guadeloupe windward coast forms and *winstoni* of Dominica.

The second cycle islands of the Lesser Antilles are generally dry. An exception is southwestern Grande Terre, which is close enough to the mountains of La Guadeloupe to be well-watered lowland. In the Guadeloupéen archipelago, two of the second cycle islands, La Désirade and Marie Galante, are high enough to get at least more rain than does northeastern Grande Terre or Les Iles de la Petite Terre. Désirade rises abruptly to elevations of nearly 300 m, and is rather high throughout. Marie Galante, on the other hand, is rather ''lumpy'' in topography, like southwestern Grande Terre, but neither high enough (*ca.* 200 m at the highest point) to collect much rain of its own nor adjacent to a mountain range that could back up rain-bearing clouds over it.

The results of the above conditions are that Désirade is fairly homogeneous in ecological conditions and wetter than northeastern Grande Terre. Marie Galante, however, is ecologically diverse, but the diversity is not in the form of geographical zones: dry country and rather lush, wet country alternate in patches all over Marie Galante. It is suggested that this complex situation with respect to ecology may account for the extreme variabiliy of *A. m. ferreus* on Marie Galante.

Further, a generalization suggests itself: wide-ranging dry country anoles are more variable than wet country anoles. This generalization would obviously not hold in cases like Les Iles de la Petite Terre and the low, dry "crescent" of Les Saintes because in these very small geographic areas the ecological conditions are fairly homogeneous. In the larger, generally dry areas, however, there are always ravines, ponds, or coastal marshes that provide patches of more or less lush vegetation, and thus ecological diversity, within the encompassing "dry country" region. If variability is a function of ecological diversity, then this generalization is valid.

ACKNOWLEDGMENTS

Without the patient assistance of Drs. H. M. Smith and E. E. Williams, who both read and reread this paper in many manuscript editions, it would probably never have seen completion. Both Messrs. Paul Bouclier and Josèph Théminé, of Point-à-Pitre, Grande Terre, assisted me greatly in getting to some of the difficult localities collected. Miss M. A. Mertz prepared the translation of the summary into French.

This work in its entirety, both in the field and in the laboratory, was supported by National Science Foundation Grant G-16066.

SUMMARY

A collection of 792 *Anolis* from 77 localities on 13 islands of the Guadeloupéen archipelago is reported on. The islands include La Guadeloupe ("Basse-Terre"), Grande Terre, La Désirade, Marie Galante, Ilet-à-Kahouanne, Ilet-à-Fajou, Ilet-à-Cochons (ou Gouvernement), both of Les Iles de La Petite Terre, and four of Les Iles des Saintes. Five previously named populations are reviewed and redefined: *marmoratus*, *alliaceus*, *ferreus*, *speciosus*, and *terraealtae*. Seven previously undescribed populations are described and named: *girafus*, *setosus*, *kahouannensis*, *inornatus*, *desiradei*, *chrysops*, and *caryae*. All twelve populations are regarded as subspecies of *Anolis marmoratus* Duméril and Bibron, 1837. The concept of Simpson's (1961) ''evolutionary species'' is utilized and discussed; criteria for determining continuity of evolutionary role among insular populations are enumerated. The role of ecological zonation in subspeciation is discussed relative to *Anolis marmoratus* and other species of the *bimaculatus* group.

SOMMAIRE

Une collection de 792 *Anolis* de 77 localités de treize îles de l'archipel Guadeloupéen est décrite. Les îles comprennent La Guadeloupe (''Basse Terre''), Grande Terre, La Désirade, Marie Galante, Ilet-à-Kahouanne, Ilet-à-Fajou, Ilet-à-Cochons (ou Gouvernement), les deux Iles de la Petite Terre, et quatre des Iles des Saintes. Cinq populations, précédemment nommées, sont revues et redéfinies: *marmoratus, alliaceus, ferreus, speciosus*, et *terraealtae*. Sept populations non-décrites auparavant sont décrites et nommées: *girafus, setosus, kahouannensis, inornatus, desiradei, chrysops*, et *caryae*. Les douze populations sont toutes considérées comme sous-espèces d'*Anolis marmoratus* Duméril et Bibron, 1837. La notion de ''l'espèce evolutive'' de Simpson (1961) est adoptée et discutée; Les critères pour la définition de la continuité du rôle evolutif de ces populations insulaires sont définis. Le rôle de la zonation écologique dans la formation des sous-espèces est considéré chez *Anolis marmoratus* et d'autres espèces du groupe *bimaculatus*.

LITERATURE CITED

DAVIS, W. M.
1926. The Lesser Antilles. Am. Geog. Soc., New York, 207 pp.

LAZELL, J. D., JR.
1962. Geographic differentiation in *Anolis oculatus* on Dominica. The anoles of the eastern Caribbean (Sauria, Iguanidae). Part V. Bull. Mus. Comp. Zool., **127**(9): 466-475.

SIMPSON, G. G.
1961. Principles of Animal Taxonomy. Columbia Univ. Press, New York, xii + 247 pp.

UNDERWOOD, G.
1959. Revisionary notes. The anoles of the eastern Caribbean (Sauria, Iguanidae). Part III. Bull. Mus. Comp. Zool., **121**(5): 191-226.

UNDERWOOD, G. AND E. E. WILLIAMS
1959. The anoline lizards of Jamaica. Bull. Inst. Jamaica, Sci. Ser., **9**: 1-48.

TABLE 1

Some color characteristics of adult males of the twelve subspecies of *Anolis marmoratus* in the Guadeloupéen archipelago.

Subspecies	Ground Color	Markings	Throat Fan Skin	Throat Fan Scales	Orbital Area
marmoratus	green + blue	orange marbling anteriorly	orange-yellow	yellow	marbled orange
alliaceus	green	light bordered, dark spots	dull orange	green	brown-green lids white
girafus	brown to green + blue	light reticulations setting off dark areas	yellow	white	brown
setosus	green + blue	dark, temporary, transverse bars	yellow	greenish	dark green
kahouannensis	chartreuse (= bright yellow-green)	none	yellow	yellow	greenish
speciosus	green + blue	none	yellow	greenish	sky blue
inornatus	dull greenish	faint transverse bars; flank stripe	yellow	white	brown
desiradei	pale grey-green	vermiculations	yellow	white	red
chrysops	pale grey-green	vermiculations reduced	yellow	yellow	red-gold
ferreus	grey-brown + green	flecking	yellow ± grey	yellow ± grey	dull-yellow
terraealtae	grey-brown + green	yellow blotches	yellow	yellow	dull-yellow
caryae	pale green	fine, pale vermiculations	yellow	yellow	cream-colored

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 12

ANOLIS EQUESTRIS IN ORIENTE PROVINCE, CUBA

By Albert Schwartz

With One Plate

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
September 15, 1964

PUBLICATIONS ISSUED BY OR IN CONNECTION WITH THE

MUSEUM OF COMPARATIVE ZOOLOGY
HARVARD UNIVERSITY

BULLETIN (octavo) 1863 — The current volume is Vol. 131.

BREVIORA (octavo) 1952 — No. 207 is current.

MEMOIRS (quarto) 1864–1938 — Publication terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 41 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 28 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained from the Publications Office of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Peters' Check-List of Birds of the World. Volumes 1, 4 and 6 are out of print; volumes 2, 3, 5, 7, 9, 10 and 15 are currently available.

Phylogeny and Evolution of Crustacea. Proceedings of a conference held at Cambridge, Mass., March 6-8, 1962. H. B. Whittington and W. D. I. Rolfe, editors. Cambridge, Mass., 192 pp., 80 figs., 1963. Cloth bound, $6.75.

Fishes of the Gulf of Maine, by Henry B. Bigelow and William C. Schroeder. Washington, viii - 577 pp., 1953. Photo-offset reprint, $6.50.

PUBLICATIONS OF THE BOSTON SOCIETY OF NATURAL HISTORY

The remaining stock of the scientific periodicals of the Boston Society of Natural History has been transferred to the Museum of Comparative Zoology for distribution. Prices for individual numbers may be had upon request.

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 12

ANOLIS EQUESTRIS IN ORIENTE PROVINCE, CUBA

By Albert Schwartz

With One Plate

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
September, 1964

Bull. Mus. Comp. Zool., Harvard Univ., 131(12): 403-428, Sept., 1964

No. 12 — *Anolis equestris in Oriente Province, Cuba*

By Albert Schwartz[1]

INTRODUCTION

In 1958, I reviewed the subspecies of the Cuban giant anole, *Anolis equestris*. At that time, the only specimens from Oriente, the easternmost Cuban province, were sixteen individuals, all in rather poor condition and most of which had been in preservation for some time. Also, of these sixteen, nine were from the northwestern coast of Oriente and represented the subspecies *thomasi*, thus leaving only seven lizards from the remainder of the province. Since that time, I have collected a series of these anoles in Oriente, under National Science Foundation grant G-6252, in the summers of 1959 and 1960; in addition, in the belief that Oriente *equestris* could best be treated as a unit and on the basis of all available material, Dr. Ernest E. Williams has invited me to study certain specimens he was intending to describe, as well as certain comparative material obtained in Cuba under NSF Grant G-16066 or borrowed by him from the Hamburg Museum. The gathering together of all this material makes it possible to clarify the Oriente picture a bit more satisfactorily, although all questions are by no means answered.

I wish to thank Ronald F. Klinikowski, David C. Leber, James D. Smallwood, and Barton L. Smith for their assistance in the field. Mr. Klinikowski has also made the illustrations for the present paper. In addition to specimens borrowed from the Museum of Comparative Zoology (MCZ), the Hamburg Museum (HM), and the American Museum of Natural History (AMNH), for which I wish to thank Dr. Ernest Williams, Dr. Werner Lädiges, Charles M. Bogert, and Dr. Richard G. Zweifel, I have examined material from the Carnegie Museum (CM) under the care of Neil D. Richmond, and the Museo y Biblioteca de Zoología de la Habana (MBZH) which was formerly under the curatorship of Miguel L. Jaume García; specimens from the United States National Museum (USNM) are currently not available, but I have previously taken scale counts and measurements on the pertinent specimens in that institution, and the loans were made at that time by Dr. Doris M. Cochran. All these curators deserve my sincere thanks for their cooperation.

---

[1] Present address: 10,000 S.W. 84th Street, Miami 43, Florida.

SYSTEMATICS

In my previous paper I referred all Oriente *Anolis equestris* (except those from the northwestern coastal region of Banes and Gibara) to the subspecies *noblei;* the Banes and Gibara material was clearly referable to the more western race *thomasi.* At the same time, I mentioned (1958:6) a bizarrely patterned individual from the Río Yateras, which lies to the east of the Bahía de Guantánamo, and commented that "additional specimens from this area would be instructive." One other fact is worthy of mention: when Barbour and Shreve (1935:250-51) described *A. e. noblei,* they had only three specimens, two of which were juveniles. The type, an adult male, is from the Sierra de Nipe, a poorly restricted locality; of the two juvenile paratypes, one is from Santiago de Cuba and the other from near Guantánamo. Although immature, the Santiago de Cuba specimen is sufficiently grown to demonstrate that it is not assignable to *noblei* but rather to the race which occurs between the Bahía de Santiago and the Bahía de Guantánamo. The Guantánamo juvenile is so young that it lacks any adult pattern and has only the uniform dorsal ground color (presently brown, but emerald green in life) with a series of four paler dorsal crossbands; this coloration is generally that of juveniles of most races of *A. equestris.*

A. e. thomasi is the giant anole of the northern Oriente coast from the Camagüey-Oriente line as far east as Banes. Remarkably, a young specimen (snout-vent length 113 mm) from Cabo Cruz (AMNH 83632) is likewise clearly of this same race (see Figure 1). There are no specimens of *A. equestris* from the interior of western Oriente, but on the basis of the Cabo Cruz and northern coastal records, the implication is clearly that *A. e. thomasi* occupies more or less the western third of Oriente. Considering the subspecific differentiation in *A. equestris* in the remainder of the province, this widespread distribution of *A. e. thomasi* is rather surprising. Considering, however, the relative uniformity of the western third of Oriente in contrast to the great ecological diversity of the balance of the province, the widespread occurrence of *A. e. thomasi* is more or less to be expected. This more western subspecies occupies the Camagüey-Tunas-Holguin subregion and the Cauto-Alto Cedro Plain (Marrero, 1951:550 *et seq.*, 636 *et seq.*). The former of these physiographic regions is that area occupied by *thomasi* in the province of Camagüey, and the latter region covers most of central western Oriente and extends from north of the Sierra Maestra south almost to Cabo Cruz.

The eastern two-thirds of Oriente, as well as the entire southern coast, is mountainous; the Sierra Maestra extends from the vicinity of Pilón on the west (near Cabo Cruz) to the Bahía de Santiago on the east; between this bay and the Bahía de Guantánamo lies the isolated but nonetheless related Sierra de Gran Piedra. The Sierra Maestra-Gran Piedra massif is bounded on the north by the valley of the Río Cauto. The remainder of the province is composed of one grand mountainous mass, variously subdivided and of varying elevations; in some areas precise names have been associated with especially prominent ranges; the Sierra de Nipe and the Sierra de Cristal are two of these, south of the Bahía de Nipe and to the south between the cities of Mayarí and Sagua de Tánamo, respectively. The eastern quarter of the province is occupied by the extremely rugged and dissected mountain mass which is customarily named the Cuchillas de Toa. The southern coast lies in the rain shadow of the Sierra Maestra, Sierra de Gran Piedra, and the Sierra de Purial (a subdivision of the Cuchillas de Toa); this coastal strip is extremely hot and xeric, with vegetation typical of such areas in the tropics — cacti, acacias, and many shrubby plants. The north coast, north of the Cuchillas de Toa, is luxuriant, and in many places the rain forest descends almost to the coastal beaches themselves. From the above brief discussion it should be obvious that much of Oriente is varied both climatically and physiographically; against such a setting it is not likely that *A. equestris*, which is tolerant of a wide variety of ecological conditions, would remain undifferentiated.

The type locality of *A. e. noblei* is the Sierra de Nipe. This range lies to the north of the valley of the Río Cauto, which separates it from the Sierra Maestra to the south. The Sierra de Nipe is the westernmost portion of the large mountain mass of eastern Oriente. Presently, there is but a single specimen (the type of *A. e. noblei*) of *A. equestris* from this area; in fact, the number of preserved *equestris* from interior localities in Oriente is very small. The type specimen (MCZ 26653) is a large adult male (snout-vent length about 152 mm); despite its length of time in preservative, the head pattern and to a lesser extent the body pattern are still decipherable. The body in life was presumably some shade of green; presently, it is green with scattered brown dots on one side and brown with scattered buffy spots on the other. These dots are actually restricted to single scales, although on occasion two or even three adjacent scales are unicolored and the "dot" is thus more extensive. The hindlimbs and the tail are obscurely banded with lighter color; these bands are again actually a vertical series of scales which are set off from the ground color and are usually only one scale in width. Using the distance between the snout and the anterior border of the eye (hereinafter called the snout-eye distance), there are 20 rows of scales vertically, and 24 rows of scales horizontally on the body included in this distance. There are 22 rows of square caudals in the snout-eye distance as well.

The top of the head is mottled dark on a light background; there is more light color than dark. From experience with *A. equestris* in life, I assume that the light coloration on the head was yellow or white, although pale green is another possibility. The pale head coloration extends posteriorly over the occiput and onto the neck, where there are two irregular pale nuchal blotches (see Figure 2). Laterally, the upper and lower labials are dark; the loreal region is dark, blending gradually into the pale canthal ridge. The canthal ridge continues pale above the eye and merges with an equally pale postorbital spot which in turn is adjacent to the nuchal spot mentioned above. There is a pale green postlabial stripe and a pale green shoulder stripe, both fairly clearly set off from the ground color. The eyeskin is pale brown. There are 11 supralabials to below the center of the eye, and about 45 subdigital lamellae on the fourth toe.

Before proceeding, it seems wise to mention the following problems as far as scale counts on these giant anoles are concerned. Barbour and Shreve (1935: 250) diagnosed *A. e. noblei* partially by means of the number of scales around the body just caudal of the dewlap. In 1958 I rejected this technique as difficult and subject to error, and adopted the snout-eye distance as a standard. The latter is still not completely satisfactory; at the time of my 1958 paper I was studying anoles principally collected and preserved by myself and party. These anoles were injected with formalin and laid out to harden in metal pans. Thus they had been subjected to more or less uniform procedures, were slightly distended with preservative, and were uncurled and straight. Most scale counts which I have taken previously were on these uniform specimens. However, when working on specimens which at times are desiccated, overly injected and distended, curled in jars, etc., I am well aware that the snout-eye count is subject to tremendous bias. Secondly, the fourth toe subdigital lamellae present a problem. I have usually counted only those subdigital scales which are distinctly broader than long and with free edges. These scales occupy roughly the three distal phalanges. But in some individuals these scales continue much farther proximally, without interruption; to count to the "normal" stopping place at the end of the third distal phalanx is difficult and subject to error, and I have continued to count these lamellae beyond this point. Such proximad extensions account for some unusually high counts.

There are at hand nine specimens of *A. equestris* from the area of the Sierra Maestra which differ in several respects from the type of *A. e. noblei.* For these lizards from the southern massif in Oriente I propose the name, in allusion to the large-headed males:

Anolis equestris galeifer new subspecies

Type: MCZ 59326, an adult male, collected near Buey Arriba, southwest of Bayamo, Oriente Province, Cuba, by Ramón Molina and Rodolfo Ruibal, 17 July 1959.

Paratypes: MCZ 59325, same data as type; AMNH 83627, Las Mercedes, 27 km S Yara, Oriente Province, Cuba, collected by Ronald F. Klinikowski, 7 July 1959; HM 5261 (4 specimens), mountains near Guisa, Oriente Province, Cuba, collected by Thumb, October, 1936; MBZH 142, near Loma del Gato, El Cobre, Santiago de Cuba, Oriente Province, Cuba, collected by C. T. Ramsden and Hno. Cristóstamo, no date; HM 5936, "Oriente," Cuba, collected by Thumb, 1936.

Distribution: Apparently the region of the Sierra Maestra from Las Mercedes on the west to Loma del Gato on the east.

Diagnosis: A subspecies of *Anolis equestris* characterized by a combination of large size, moderately-sized dorsal and caudal scales without white skin streaking; unspotted dorsum; a prominent pale postorbital blotch but no nuchal extension thereof; a short and indistinct postlabial stripe and a prominent and long shoulder stripe; dewlap pink.

Description of type: An adult male with both hemipenes extruded, snout-vent length 183; tail 340 (all measurements in millimeters); dorsals (counted vertically) in snout-eye distance, 19; dorsals (counted horizontally) in snout-eye distance, 21; caudals (counted horizontally) in snout-eye distance, 23; supralabials to below center of eye, 10; enlarged scales on undersurface of fourth toe, 47.

Head longer (54.0) than broad (34.2), snout rather acuminate but rounded; canthus rostralis of six enlarged and peaked scales; 38 loreals on one side, the uppermost row more or less rugose, the remainder smooth; dorsals quadrate, subquadrate or even rectangular, separated by numerous tiny scales; 29 enlarged dorsals between slightly smaller and more regular belly scales and medial dorsal row of flaccid crest scales, largest midway between fore- and hindlimb insertions on sides; about 31 smaller scales on belly between lowermost rows of enlarged laterals, gradually increasing in size from midventer laterally; dorsal surface of limbs covered with pavement-like scales about two-thirds the size of enlarged laterals; ventral surface of limbs covered with scales about one-half the size of midventrals; ventral edge of dewlap with scales considerably smaller than midventrals, largest anteriorly.

Coloration: The preserved specimen is bluish dorsally and dark brown laterally; there is no indication on the dorsum, limbs, or tail, of any dotting, spotting, or crossbanding. The ground color of the limbs is blue, as is that of the tail. The dewlap still has a faint pink tinge and the venter varies from a bluish cream to brown. I gather from the present coloration that this lizard was green in life, with no spotting or crossbanding. The casque is presently dark brown with a minimum of paler spotting; there are a few isolated spots on the snout and a few on the occipital region. The canthus is pale and expands posteriorly into a prominent postorbital blotch (see Figure 3). The labials, lores, and eyeskin are dark brown. The postlabial stripe is short and indistinct, and the shoulder stripe is long, dark gray, and likewise indistinct.

Variation: The paratypes include four males, two females. and two juveniles: the entire assemblage varies in snout-vent length from 89 to 173, two of the paratypic males reaching the larger dimension. The type is, as previously noted, larger than either of these two males. Of the males, the three adults resemble the type closely in pattern; none is spotted, the postlabial stripe is indistinct, and the shoulder stripe is long and fairly prominent. All have a pale canthus and boldly delineated postorbital blotch. The top of the casque is about as described for the type in one specimen (HM 5261), whereas the remaining two adult males have the casque marked with somewhat more pale areas, with always more dark than light pigmentation. There is never an extension of the pale area onto the nuchal region, although all four male paratypes show at least an indication of a single pale nuchal spot; one specimen has a few scattered pale nuchal blotches which are not especially well defined. The young male (MBZH 142) has the casque somewhat indistinctly marbled. This lizard also lacks a postorbital blotch. The two females show much the same variation as the males, although both have postorbital blotches and some indistinct neck blotching. The shoulder stripe is poorly defined and the labial stripe is likewise not especially prominent, although it is discernible. The two juveniles also show the postorbital blotch; in these lizards the postlabial and shoulder stripes are more prominent than in adults. The dorsal scales vary vertically between 17 and 24, vary horizontally between 19 and 28, and there are between 44 and 61 fourth toe lamellae.

Although I have grouped the comparisons of the Oriente subspecies of *A. equestris* at the end of the present paper, it is appropriate here to compare *A. e. galeifer* with *A. e. noblei*. From the outset it should be obvious that such comparison is greatly hampered by there being available but a single specimen of *noblei*, as presently defined — i.e., the type. *A. e. galeifer* differs from *noblei* in having distinctly larger dorsal scales; there are 20 in the snout-eye distance vertically and 24 horizontally in the type of *noblei*. These figures are within the known range of *galeifer;* however, inspection of the scales of the type of *noblei* shows that they are distinctly smaller than those of comparably sized specimens of *galeifer*. In this case, observation is more useful than actual employment of the vernier: my comments on differences in preservation methods of these specimens in a foregoing paragraph are most pertinent.

In addition, the pattern of the two races is distinctive: no *galeifer* has extensive nuchal blotching as does *noblei*. *A. e. noblei* is dotted dorsally and has crossbanded limbs and tail; *galeifer* does not. The extensive postlabial stripe in *noblei* contrasts with the absence or reduction of this stripe in *galeifer*. The shoulder stripe is narrow and long in *galeifer*, but is broad and long in *noblei*.

The dewlap coloration in *noblei* is unknown; presently, the dewlap of the type is a faded yellow but this is not trustworthy since Barbour and Shreve (1935:251) noted that the dewlap of the type was at the time of their description decidedly pinkish, a much more likely coloration. I have seen one *A. e. galeifer*, the female from Las Mercedes, in life; the dewlap coloration of this lizard was noted as pink. I assume that both *noblei* and *galeifer* have pink dewlaps; there may of course be a difference in precise shade.

The situation involving these two subspecies is complicated due to the absence of an adequate sample of *noblei.* However, the occurrence of one race of *A. equestris* in both the Sierra de Nipe and the Sierra Maestra is not likely zoogeographically. The former is separated from the latter by the valley of the Río Cauto; the form of *A. equestris* in this valley is presently unknown. It is not improbable that *A. e. thomasi* occurs there (as noted above), or the valley may be a region of intergradation between *noblei* and *galeifer.*

I have previously examined one specimen (USNM 29784) which may possibly be associated with *galeifer.* This lizard, an adult female, snout-vent 150, is from Guamá and is presently not available. My notes indicate that it is unspotted (and thus not assignable to the race described below, nor with the dotted *noblei*), and that it likewise had no shoulder spots. The village of Guamá was located about 40 miles due west of Santiago de Cuba, near the coast (Stejneger, 1917: 260). The dorsal scales of the lizard number 19 vertically and 23 horizontally, and thus are within the known range of *galeifer.* If the mining camp of Guamá was actually in the Sierra Maestra or the foothills of this range, it is most probable that this specimen is representative of *A. e. galeifer.* It should be re-inspected to determine its subspecific status; for the moment I regard it tentatively as *A. e. galeifer.*

The southern Oriente coast between Cabo Cruz and Cabo Maisí has been shown to harbor a number of races of iguanid lizards of the genus *Leiocephalus* (Hardy, 1958; Schwartz, 1960); two coastal features which seem to have an isolating effect on lizard populations in this region are the Bahía de Santiago and the Bahía de Guantánamo. The same features have played a role in differentiation of *A. equestris* along the xeric coast. In the area between these two bays, a very distinct subspecies of the Cuban giant anole has developed. I take pleasure in naming this form for James D. Smallwood who collected the greater portion of presently available specimens, as:

ANOLIS EQUESTRIS SMALLWOODI new subspecies

Type: AMNH 89526, adult male, from Laguna de Baconao, Oriente Province, Cuba, James D. Smallwood collector, 9 August 1960. (Original number 9761.)

Paratypes: AMNH 89525, 9.4 mi. W Laguna de Baconao, Oriente Province, Cuba, J. D. Smallwood collector, 9 August 1960; AMNH 89527-30, Laguna de Baconao, Oriente Province, Cuba, J. D. Smallwood collector, 17 August 1960.

Distribution: Xeric coast between the Bahía de Santiago and the Bahía de Guantánamo, Oriente Province, Cuba; see, however, discussion below.

Diagnosis: A subspecies of *Anolis equestris* characterized by a combination of moderate size, moderately-sized dorsal and caudal scales without white skin streaking, leopard spotted dorsum (the spots encompassing as many as six adjacent scales and becoming elongate and linear anteriorly), a pale green postlabial stripe and pale greenish-yellow occiput, dewlap pink.

Description of type: An adult male, snout-vent length 155; tail 298; dorsals (counted vertically) in snout-eye distance, 19; dorsals (counted horizontally) in snout-eye distance, 22; caudals (counted horizontally) in snout-eye distance, 26; supralabials to below center of eye, 9; enlarged scales on undersurface of fourth toe, 48.

Head longer (45.3) than broad (30.0), snout rounded; canthus rostralis of six enlarged rugose and peaked scales; 26 smooth loreals on one side; dorsals quadrate or subquadrate, separated by numerous tiny scales; 23 enlarged dorsals between slightly smaller and more regular belly scales and medial dorsal row of flaccid crest scales, largest midway between fore and hindlimb insertions on sides; about 29 smaller scales on belly between lowermost rows of enlarged laterals, gradually increasing in size from midventer laterally; dorsal surface of limbs covered with pavement-like scales about one-third to one-half the size of enlarged laterals; ventral surface of limbs covered with scales comparable in size to midventrals; ventral edge of dewlap with scales slightly smaller than midventrals, largest anteriorly.

Coloration: In life, dorsum green with pale green leopard-like spotting, the spots involving as many as four adjacent scales and well separated from one another, and becoming linear on the anterior third of the body; eyeskin greenish gray; a pale green postlabial stripe onto the neck, bordered above and below by darker green and sharply and prominently delimited both above and below; shoulder stripe bright yellow; top of head greenish yellow, the occipital area pale pea-green with scattered dark green blotches; lores pale green mottled with dark green (see Figure 4); scales on throat and anterior portion of dewlap dark green; dewlap pink (Pl. 2A9; color designations from Maerz and Paul, 1950). Hindlimbs with pale green transverse lines, which are also partially indicated proximally on the tail. Venter dark green.

Variation: The paratypes include two males and three females, varying in snout-vent length from 144 to 159. Coloration of the series is remarkably uniform. A female from 9.4 mi. W Laguna de Baconao had a dewlap which was Pl. 1F9 in life (Maerz and Paul); the dewlaps in the remainder of the series were noted as grading from faintly orange to pink. All are spotted, although the spotting varies in extent; I cannot detect any difference in spotting between the sexes. The elaborate head pattern is manifested in all, although one female shows it a little less prominently than the remainder of the lot. The dorsal scales vary vertically between 18 and 21, vary horizontally between 18 and 22; caudal scales vary between 23 and 26, and there are between 48 and 51 fourth toe lamellae. Inspection of the above data shows that, at least in this restricted sense, *A. e. smallwoodi* is a small, compact group of lizards with very limited variation in coloration and scalation.

As one progresses away from the immediate coastal area between the two bays — the type locality of *smallwoodi* — the situation becomes more complex. There are seven additional specimens from this general area which require some comments.

There is a single juvenile (AMNH 89532, snout-vent 61) from Playa Juraguá which, when collected, still had the vivid green dorsal coloration with four creamish-white dorsal bands partly broken into spots. Playa Juraguá lies 3.7 mi. east of Siboney, and is thus to the east of the Bahía de Santiago; I regard this specimen as *smallwoodi* purely on the basis of provenance. It is possible that the broken condition of the dorsal bands is a characteristic of juvenile *smallwoodi;* on the other hand, the broken bands may be merely a transition stage between juvenile and adult patterns.

Two specimens from Santiago de Cuba (MCZ 6924; USNM 58855) and one from 4 km north of Santiago de Cuba (AMNH 89531) are instructive. One of these is a young lizard (snout-vent 97) which shows the dark dorsal coloration and light crossbands, but in addition clearly shows the pale occiput and incipient dorsal spotting characteristic of *smallwoodi.*

The second Santiago de Cuba specimen (USNM 58855) is a young female; the specimen is presently not at hand, but I have previously examined it. My notes indicate that it has a light nuchal spot behind the occiput and a shoulder spot which is represented by only its own small dark border. There is no mention of any dorsal spotting, pale occipital patches, pale postlabial line, etc. — in fact, nothing to ally it to *A. e. smallwoodi.*

In addition, the dorsal and caudal scale counts (vertical, 10; horizontal, 17; caudal, 13) are extremely small and completely outside the known variation of *smallwoodi*. Likewise it cannot be regarded as *noblei* or *galeifer* for reasons of scalation. I can only surmise that this individual is not from Santiago, nor for that matter from Oriente; additional inspection is imperative.

The third Santiago specimen is from 4 km north of the city, and thus is in the foothills of the Sierra de Boniato at an elevation of approximately 1000 feet (*ca.* 300 m); this specimen was seen alive by myself. It is a young female (snout-vent 138) which was green in life with the old juvenile bands still present and orange in color. Between the juvenile bands there are vertical rows of spots; the hindlimbs are banded as is the base of the tail. All the above might well be *smallwoodi* characteristics. The head, however, is dark dorsally, the occipital region is only slightly paler than the dorsum and the postlabial line, although prominent, is not so light nor so prominent as in *smallwoodi*. The shoulder stripe likewise is somewhat more prominent than in *smallwoodi*. Vertical dorsals are 19, and thus within the limits of *smallwoodi*. I suspect that, despite the absence of the occipital pale areas (a feature which we know from the juvenile specimen discussed above appears very early in life), this lizard should be regarded as the coastal form. Some of its peculiarities may be due to the influence of the adjacent *galeifer* or another, more northern rather than western, form, as yet unknown.

A fine well preserved adult male (MBZH 260) from Hongolosongo is another puzzle. Hongolosongo lies to the west northwest of El Cobre and is on the *northern* slope of the Sierra del Cobre to the *west* of the Bahía de Santiago. I have no doubt that this individual is referable to *smallwoodi;* it possesses the pale head and occiput, dorsal spots, etc., and the scales are completely within the range of topotypic *smallwoodi*. If we assume that the two available specimens from the area of Santiago de Cuba (eliminating the single peculiar USNM specimen as noted above) represent *smallwoodi*, then clearly there is no gap between coastal specimens from east of the Bahía de Santiago and the single individual from Hongolosongo. It is remarkable, however, that a lizard which occurs in the xeric coastal plain in this region should also occur on the north side of a somewhat removed range of mountains, but such indeed seems to be the case. Apparently the races *smallwoodi* and *galeifer* intergrade somewhere between Loma del Gato and Hongolosongo, a distance of about thirty miles.

There are two available specimens from the coast (or nearly so) west of the Bahía de Santiago. One of these (USNM 29784) from Guamá has already been commented upon under the discussion of *A. e. galeifer,* with which race I temporarily associate it. The absence of dorsal spotting disqualifies it at once as being *smallwoodi.* The other lizard (MCZ 42480) is a juvenile (snout-vent 50) from the coast south of Pico Turquino. It shows the typical juvenile pattern and coloration, and there is nothing distinctive about it. Since it is coastal (P. J. Darlington coll.), it may be assignable to *smallwoodi.* Only additional specimens from this region will allow a definite subspecific allocation.

When in 1958 I examined the available material from Oriente, there was a single specimen from the Río Yateras (CM 33320) which was so unusually patterned that it was only with extreme uncertainty that I assigned it to *noblei.* Since that date, another such specimen has come to light (MCZ 68921). In addition, I have examined still another specimen which I regard as belonging to this same heavily spotted form, for which I propose the name *palardis* as an anagram of the Latin word *pardalis,* meaning "leopard."

ANOLIS EQUESTRIS PALARDIS new subspecies

Type: CM 33320, adult male, Río Yateras, 5 mi. north of the river mouth, Oriente Province, Cuba, Wm. McLane and R. H. Wilkinson, collectors, 16 September 1952.

Paratype: MCZ 68921, Guantánamo (U. S. Naval Base), Oriente Province, Cuba, R. Lando, collector, 1962.

Distribution: Apparently the Guantánamo Basin and eastward along the southern Oriente coast presumably at least as far as Baitiquirí.

Diagnosis: A subspecies of *Anolis equestris* characterized by a combination of moderate size, moderately-sized dorsal and caudal scales without white skin streaking, heavily spotted or almost reticulate dorsum, the spots encompassing as many as fourteen adjacent scales and parts thereof and becoming elongate and linear anteriorly, prominent pale postlabial and shoulder stripes, a prominent pale postocular patch, upper surface of casque dark with discrete pale flecking or with more extensive pale marbling.

Description of type: An adult male, snout-vent length 150; tail (incomplete and regenerating) 120; dorsals (counted vertically) in snout-eye distance, 14; dorsals (counted horizontally) in snout-eye distance, 16; caudals (counted horizontally) in snout-eye distance, 14; supralabials to below center of eye, 10; enlarged scales on undersurface of fourth toe, 59.

Head longer (45.0) than broad (28.0), snout rounded; canthus rostralis of six enlarged rugose and peaked scales; 32 smooth loreals on one side; dorsals quadrate to subcircular, separated by numerous tiny scales; 28 rows of enlarged dorsals between slightly smaller and more regular belly scales and medial dorsal row of flaccid crest scales, largest midway between fore- and hindlimb insertion on sides; about 36 smaller scales on belly between lowermost rows of enlarged laterals, the midventral scales only slightly smaller than the lower row of laterals; dorsal surface of limbs covered with pavement-like scales about one-third to one-half the size of enlarged laterals; ventral surface of limbs covered with scales two-thirds the size of midventrals; ventral edge of dewlap with scales slightly smaller than midventrals, largest anteriorly.

Coloration: The preserved specimen is almost chocolate brown, the entire dorsum covered with rather large and very prominent pale spots, the largest encompassing six adjacent scales; both fore- and hindlimbs are crossbanded with pale buffy, and the proximal portion of the tail is especially prominently crossbanded with narrow bands one to three scales in width. The dorsal surface of the head is dark brown with clear and discrete white flecks scattered more or less uniformly; the occiput is dark with a few white flecks like those on the casque, and these extend onto the neck where there is a single larger white spot. The canthus and eyeskin are pale and there is a conspicuous and clearcut white postorbital blotch; the postlabial stripe is somewhat less prominent and the shoulder stripe is very long, not quite so pale, and extends almost half-way along the body beyond the forelimb insertion (see Figure 5). There is a peculiar pale U-shaped figure over the sacrum which is washed with brown and which even now stands out conspicuously among the large dorsal spots. The ventral surface is dark; both supra- and infralabials are dark centered and pale edged; the throat is more or less clouded longitudinally with dark brown. The dewlap is presently entirely white.

Variation: The single paratype is a rather poorly preserved adult male with a snout-vent length of 168. The coloration and pattern resemble those of the type very closely except that the body spots are even larger and more extensive, involving as many as fourteen adjacent scales. The limbs and tail are boldly banded, the bands on the tail as wide as three caudal scales. The casque is likewise more prominently spotted than that of the type. Other head and stripe details are comparable between the two, except that the postlabial and shoulder stripes are paler and thus show more contrast with the almost black ground color. The dewlap is still faintly pink. Scale counts on the paratype are: vertical dorsals, 18; horizontal dorsals, 24; caudals, 24; fourth toe lamellae, 45. The difference in size of dorsals between the type and paratype is doubtless an artifact of preservation since by inspection the size of the dorsals does not seem to differ strikingly.

As with *A. e. smallwoodi*, once the immediate region of the type locality is left, the specimens become problematical. There are available five other lizards which in theory should be assignable to *palardis*. Each will be discussed separately.

There is a young adult male (MCZ 42552) from Imías, which lies about 35 miles to the southeast of Guantánamo, on the coast; this locality is the farthest east from which *A. equestris* is known. I find it very difficult to assign this individual to *palardis*, to which race it might reasonably be expected to belong on the basis of geography. The body shows no signs of spotting of any sort; on the other hand, there is a large, conspicuous, dark bordered nuchal spot, and some dissociated spots on the occipital region. The casque is apparently marbled as in *palardis*, however. There is a pale postorbital spot, a pale and prominent postlabial stripe, and a fairly well expressed shoulder stripe, although the latter is not so bold nor so clear as that in *palardis*. Also, the dorsal scales are much smaller than are those of any specimens of *palardis*. There are two possibilities: 1) the lizard came from the mountains to the north of Imías, and thus represents still another Oriente race; 2) the lizard came from the coast at Imías and there is another subspecies of *A. equestris* along the southern Oriente coast beyond Baitiquirí, and thus including Imías. I prefer to believe that the former is the correct interpretation. It is even conceivable that *A. e. galeifer* extends this far east throughout the southern Oriente mountains. The Imías lizard in some pattern details resembles the more western race. However, the small size of the scales prevents this specimen from being associated with *galeifer*.

An adult female from Baitiquirí (MCZ 42551) agrees very well with the type and paratype insofar as head pattern is concerned, and in fact seems to combine the casque flecks of the type with the more blotchy casque markings of the paratype. The body is not particularly spotted; with a little imagination one can visualize the remnants of spots on the back and sides, but if they were present, they were probably not so vivid and prominent as described above. At least the neck is marked with elongate pale blotches and streaks very comparable to those of the paratype. I regard this specimen as *palardis*.

Three specimens from the environs of Guantánamo (MCZ 8977, a juvenile, snout-vent 47, from "near Guantánamo"; USNM 58057, an adult female, and MCZ 57928, an adult male, both from Guantánamo) are especially puzzling. Of these the juvenile lacks any characteristics which would align it with *palardis;* it is interesting, however, in that, of the few juveniles available from Oriente, it alone has a prominent pale green postlabial stripe. USNM 58057 is not available at the moment, but my notes on it state that it has a large and elaborate shoulder spot; obviously the specimen is not entirely spotted as are the type and paratype of *palardis*. The presence of the shoulder spot may again indicate the same situation as noted above for the Baitiquirí specimen, i.e., a remnant of the more extensive pattern.

The final Guantánamo specimen, MCZ 57928, is distinctly different from the typical material. The casque is entirely marbled with pale color. The postorbital spot is absent but there is a brown patch in the area bounded above by a raised patch of pale scales; the postlabial and shoulder stripes are not pale or especially prominent, and the dorsum shows only faint indications of having been spotted in life. Again, if this specimen came from "Guantánamo" in a broad sense only, and not from the lowlands in the Basin itself, it is likely that it is not *palardis* but some other race from the mountains to the north. I regard it only provisionally as *palardis*.

In the summer of 1959, I secured three *A. equestris* from Baracoa on the northeastern coast of Oriente. The dewlap coloration of these lizards was so very distinct that it was obvious they represented a new subspecies; Dr. Williams had also come to the same conclusion based upon three specimens in the collection at Harvard, but he has graciously allowed me to describe this new race as:

ANOLIS EQUESTRIS BARACOAE new subspecies

Type: MCZ 57404, adult female, Baracoa, Oriente Province, Cuba, P. A. Adams, collector, 4 April 1958.

Paratypes: MCZ 47050, Joar, Baracoa, Oriente Province, Cuba, G. Canet, collector, 1943; AMNH 83628, Baracoa, Oriente Province, Cuba, native collector, 11 August 1959; AMNH 83629-30, Baracoa, Oriente Province, Cuba, native collector, 13 August 1959.

Distribution: Known only from the type locality.

Diagnosis: A subspecies of *Anolis equestris* characterized by small size, extremely small dorsal scales and long dorsal crest scales, dorsum either plain green or green with pale blue small dots or flecks, a small and relatively inconspicuous postorbital patch, shoulder stripe and postlabial stripe inconspicuous and short, dewlap bluish-green.

Description of type: An adult female, snout-vent 158, tail 186, regenerated tip; dorsals (counted vertically) in snout-eye distance, 26; dorsals (counted horizontally) in snout-eye distance, 33; caudals (counted horizontally) in snout-eye distance, 29; supralabials to below center of eye, 9; enlarged scales on undersurface of fourth toe, 42.

Head longer (43.7) than broad (25.0), snout rounded; canthus rostralis of six enlarged rugose scales; about 36 smooth loreals on one side; dorsals subcircular, separated by numerous tiny scales; dorsal crest scales elongate; 38 enlarged dorsals between slightly smaller and more regular belly scales and medial dorsal row of flaccid crest scales, largest midway between fore- and hindlimb insertions on sides; about 30 smaller scales on belly between lowermost rows of enlarged laterals, gradually increasing in size from midventer laterally; dorsal surface of limbs covered with pavement-like scales about two-thirds the size of enlarged laterals; ventral surface of limbs covered with scales about one-half the size of midventrals; ventral edge of dewlap with scales one-half the size of midventrals, not appreciably enlarged anteriorly.

Coloration: In preservation, dorsum pale bluish-gray dotted with pale spots which are more or less linear and involve as many as four longitudinally adjacent scales. Dorsal surface on hindlimbs rather obscurely crossbarred with darker; forelimbs with a few pale scales which apparently indicate crossbands in the living animal. Casque pale blue dorsally with no pale markings; a pale blue postorbital blotch, a very indistinct postlabial stripe and a fairly extensive dark shoulder stripe (see Figure 6). Loreals and supralabials marbled with dark blue; throat clouded with dark; venter immaculate pale blue.

Variation: The four female paratypes vary in snout-vent length from 120 to 145, and are thus all smaller than the type. One (AMNH 83628), the smallest, is colored quite comparably to the type; another (AMNH 83630) is very dark and is flecked with isolated and discrete tiny dots dorsally; the remaining two specimens are bluish-gray dorsally without any dots or flecks, but show some irregular pale nuchal areas, and one of these has a fairly bold and prominent postorbital patch. In none are the postlabial and shoulder stripes really well defined. In the three live specimens which I have seen, the dewlap color was noted as blue or blue-green. It is unfortunate that all the specimens of *baracoae* are females, but judging from my experience with other races, the dewlap coloration is very close in the two sexes.

The small size of the dorsal scales is manifested in the following figures: vertical dorsals, 25 to 27; horizontal dorsals, 23-26; horizontal caudals, 20-29.

In addition to the type and paratypes, I have seen one juvenile (MCZ 42520, snout-vent 48); interestingly, the dorsals on this small lizard are indeed tiny and thus conform with the small scales of *baracoae.* Also, the lizard shows none of the dorsal crossbars which are usually typical of very young *A. equestris.* This patternless condition may be a character of juvenile *baracoae.*

It is appropriate here to discuss one other lizard from the environs of Baracoa. It is an adult female (AMNH 83631), snout-vent 160, from 8 miles northeast of Felicidad. This locality lies more or less equidistant between Guantánamo on the south and Baracoa on the north. The lizard might be reasonably supposed to be assignable either to *baracoae* or to some intergradient population between *baracoae* and *palardis.* The former is certainly not the case, since the dewlap was recorded in life as being pink. Likewise my color notes in life (dorsum green with light green dots which turned brown after death; head brown with cream colored casque, flecks extending onto the nape and a few on dorsal crest scales; lips, labial stripe and shoulder stripe bright green; no occipital or shoulder blotches; dewlap scales pale yellow on a pink — Pl. 1E7 — skin) indicate that this lizard was not colored as is *baracoae.* The dorsal scales (vertical 23; horizontal, 21) are also perceptibly bigger than in *baracoae* and the dorsal crest scales are not high and elongate. In some ways this specimen resembles MCZ 57928 from Guantánamo, but it is just as distinctly different. I regard it *pro tem* as a representative of a race from the mountains of interior of eastern Oriente.

Four specimens of *A. equestris* from the region of Moa on the north Oriente coast represent still another indigenous subspecies, which may be called, in allusion to the pebbly appearance of the dorsal surface of the casque:

ANOLIS EQUESTRIS SAXULICEPS new subspecies

Type: HM 5376, adult female, Moa, Oriente Province, Cuba, Thumb, collector, between April and November, 1938.

Paratypes: HM 5376 (smaller of two specimens bearing this number), same data as type; HM 5374, same data as type; MCZ 59324, *ca.* 7 km E Moa, Oriente Province, Cuba, R. Molina and R. Ruibal, collectors, 21 July 1959.

Distribution: Known only from the immediate environs of Moa.

Diagnosis: A subspecies of *Anolis equestris* characterized by a combination of moderate size, moderately sized dorsal and caudal scales without white skin streaking, dorsal coloration apparently somewhat dotted or spotted, prominent and dark bordered postlabial and shoulder stripes, absence of postorbital blotch, dorsal surface of casque with a reticulate or marbled appearance, spotted labials, dewlap pink.

Description of type: An adult female, snout-vent length 146; tail 187; dorsals (counted vertically) in snout-eye distance, 20; dorsals (counted horizontally) in snout-eye distance, 21; caudals (counted horizontally) in snout-eye distance, 24; supralabials to below center of eye, 10; enlarged scales on undersurface of fourth toe, 44.

Head longer (42.2) than broad (25.9), snout rounded; canthus rostralis of 6 enlarged rugose scales; 43 loreals on one side, smooth except that the two upper rows are somewhat rugose; dorsals subquadrate, separated by numerous tiny scales; 29 enlarged dorsals between slightly smaller and more regular belly scales and medial dorsal row of flaccid crest scales, largest midway between fore- and hindlimb insertions on sides; about 33 smaller scales on belly between lowermost rows of enlarged laterals, gradually increasing in size from midventer laterally; dorsal surface of limbs covered with pavement-like scales about one-half the size of enlarged laterals; ventral surface of limbs covered with scales about one-half the size of midventrals; ventral edge of dewlap with scales slightly smaller than midventrals, not appreicably larger anteriorly.

Coloration: The type is now dark brown dorsally, and dirty bluish gray ventrally. The middorsal area has a few scattered light blue scales, and there is a faint indication of at least two vertical lateral bands of buffy scales between the limbs. I do not know exactly what the significance of these details is, having never seen *saxuliceps* in life. It is possible that dorsally the lizard was green in life with some middorsal paler flecks and a pair of pale green lateral bars, all of which likely were rather inconspicuous. The hindlimbs are unmarked, whereas the forelimbs and dorsal surface of the hand show some paler scales, which at least on the forearm are organized into crossbands. The most striking feature is the gravelly appearance of the casque. Each scale on the dorsal surface of the casque is pale centered and dark edged, giving the casque a more or less uniformly marbled or even reticulate appearance; this pattern continues posteriorly over the top of the head as far as the occiput and into the postorbital region (which is indistinctly and finely marbled), then blends imperceptibly into the dorsal body dotting mentioned above. The lores, supra- and infralabials are likewise pale with much dark marbling, the dark pigment on the labials being placed at the sutures between the scales, rather than in the center of the scales (see Figure 7). The eyeskin is dark brown. The mental area is dull blue, grading quickly to very dark brown at about the level of the anterior edge of the dewlap, and this brown coloration continues posteriorly to the forelimb insertion. The dewlap skin is presently dirty cream. The postlabial line is pale blue, clearest anteriorly but still very obvious and bordered above and below with darker on the neck. The shoulder stripe resembles the postlabial stripe in clearness, definition, and in being bordered with darker above and below.

Variation: The three paratypes are females, one of which is rather immature, ranging in snout-vent length from 112 to 132. As far as head pattern is concerned, all resemble the type very closely. The same is true of body pattern and coloration, except for the smallest (HM 5374). This young female has a streaked dorsum, the individual streaks involving three scales on the body itself, and more in the scapular region. The neck is almost reticulate, there being more pale than dark areas. Whether this peculiar pattern reflects the juvenile pattern or whether such a condition is merely a part of the variation of *saxuliceps* is unknown. Certainly there is no doubt that this individual represents this taxon; the casque pattern is diagnostic.

The paratypes vary scalewise in that there are between 18 and 23 dorsals vertically, between 23 and 27 horizontally; caudals range from 24 to 25, and fourth toe scales between 44 and 50.

The dewlaps in two of the specimens of *saxuliceps* are still faintly pink. I assume that, despite the fact that all known *saxuliceps* are females, the dewlap coloration in males is pinkish. This coloration is quite different from the blue-green dewlap of *baracoae* to the east.

COMPARISONS AND DISCUSSION

With the description of five new races of *Anolis equestris* from Oriente, there are now nine subspecies from Cuba and another *(hassleri)* from the Isla de Pinos. Rather than inserting the comparisons between the named forms in their proper places in the descriptions, I am amassing them here for greater simplicity. Table 1 shows the range of scalation of the ten forms.

Table 1

Dorsal and caudal scale characteristics of ten populations of *Anolis equestris.*

Subspecies	No.	Dorsals (vertical)	Dorsals (horizontal)	Caudals (horizontal)
luteogularis	40	14-22	16-22	19-28
equestris	42	10-19	10-17	14-22
thomasi	17	7-11	7-12	11-17
noblei	1	20	24	22
galeifer	9	17-24	19-28	21-26
smallwoodi	6	18-21	18-22	23-26
palardis	3	14-18	16-24	12-24
baracoae	6	25-27	23-33	20-29
saxuliceps	4	18-23	21-27	24-25
hassleri	4	15-19	16-21	19-23

The races *smallwoodi, palardis,* and in some cases *baracoae* and *saxuliceps,* all differ from *thomasi* in that they possess spotted dorsa; *thomasi* never has such a feature and is characterized by white longitudinal streaking instead. Also *thomasi* is characterized by having exceptionally large scales, whereas all the new Oriente races are smaller scaled, with *baracoae* at the extreme. From *A. e. equestris* the Oriente races differ in dewlap color *(baracoae),* dorsal spotting *(smallwoodi, palardis),* and head and casque pattern *(saxuliceps, noblei, galeifer).* In addition, *baracoae* at least is completely separable from the race *equestris*

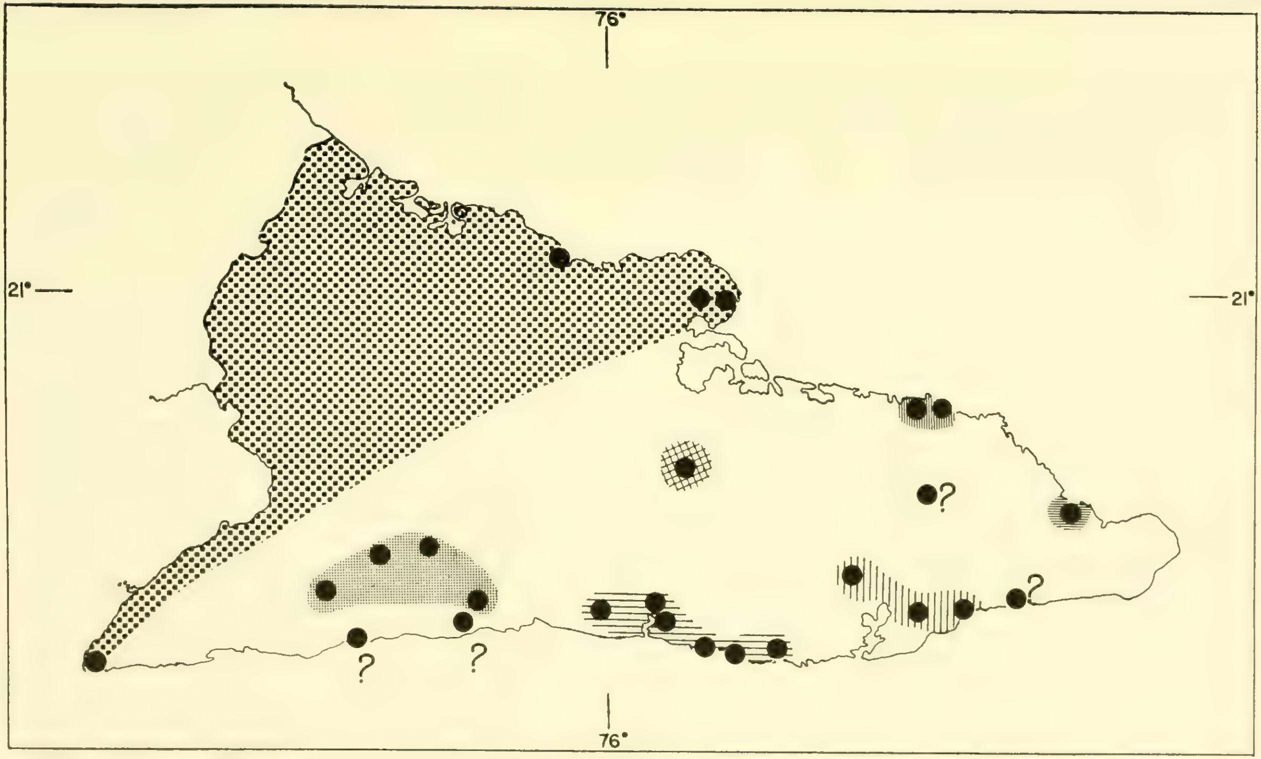


Figure 1. Map of Oriente Province, Cuba, showing the range of the subspecies of *Anolis equestris*, as follows: ***thomasi***, coarse stippling; *galeifer*, fine stippling; *smallwoodi*, horizontal coarse lines; *palardis*, vertical coarse lines; *baracoae*, horizontal fine lines; *saxuliceps*, vertical fine lines; *noblei*, crosshatching. Localities which are questioned are those of specimens which are presently not assignable to any of the above forms.

on size of dorsals; *smallwoodi* and *saxuliceps* are practically separable from *equestris* on this same character, although there is a small amount of overlap.

From *luteogularis,* a dotted form in extreme western Cuba ("with scattered specks of pale yellow on a green background," Schwartz, 1958: 5-6), the spotted Oriente races *(smallwoodi, palardis)* differ in much larger *spots* on the dorsum (in contrast to *flecks* which involve only part of a scale rather than several adjacent scales); *baracoae* differs in a blue-green rather than orange or pale yellow dewlap and much smaller dorsals; *noblei, galeifer, saxuliceps* differ in much more complex head patterns.

The five new Oriente subspecies may be differentiated as follows: 1) *baracoae* has small dorsals and a blue-green dewlap; 2) *smallwoodi* is spotted dorsally and has the occipital region pale green; 3) *palardis* has heavy, almost reticulate, dorsal spotting without pale occiput and with a pale postorbital patch; 4) *saxuliceps* has a marbled or reticulate casque, spotted lores and labials, and lacks a postorbital blotch; 5) *galeifer* is unspotted, with a pale postorbital blotch without a nuchal extension. For detailed comparison of *galeifer* with *noblei,* see the discussion of the former form. *Noblei* differs from the remaining Oriente races in having a pink dewlap (blue-green in *baracoae*), having small dorsal dots (in contrast to heavy spotting in *smallwoodi* and *palardis*), having a mottled casque rather than a marbled or quasi-reticulate one (as in *saxuliceps*), and from all Oriente races grouped together in having a nuchal extension of the pattern of the casque and occiput.

It is obvious that there still remain many problems in the distribution of *A. equestris* in Oriente. We have no real data on the area of intergradation (or even the precise distributional relationships) of *thomasi* with any of the Oriente races. The distribution and variation of *noblei* is unknown. The precise situation in the environs of the cities of Santiago de Cuba and Guantánamo is confused, due probably to improper labeling of specimens and lack of distinction between specimens taken *in* the cities and *near* them, especially in the foothills and mountains to the north. The identity of the race along the southern coast between Cabo Cruz and the Bahía de Santiago is indeterminate. Specimens are badly needed from the central portion of the mountain massif in the eastern part of the province, the single individual from near Felicidad and the one from Imías give promise of increased complexities in this region.

SPECIMENS EXAMINED

(All from Oriente Province, Cuba)

Anolis equestris thomasi (10): Gibara, 3 (A. Schwartz collection 285); Banes, 4 (AS 286); Los Angeles, 5 mi. E Banes, 2 (MCZ 25153-54); Cabo Cruz, 1 (AMNH 83632).

Anolis e. noblei (1): Sierra de Nipe (MCZ 26653).

Anolis e. galeifer (9): nr. Buey Arriba, SW Bayamo, 2 (MCZ 59325-26); nr. Loma del Gato, 1 (MBZH 142); Las Mercedes, 27 km S Yara, 1 (AMNH 83627); mountains near Guisa, 4 (HM 5261); "Oriente," 1 (HM 5936). Guamá, 1 (USNM 29784) is questionably associated with *galeifer*.

Anolis e. smallwoodi (10): 9.4 mi. W Laguna de Baconao, 1 (AMNH 89525); Laguna de Baconao, 5 (AMNH 89526-30); Hongolosongo, 1 (MBZH 260); Playa Juraguá, 1 (AMNH 89532); Santiago de Cuba, 1 (MCZ 6924); 4 km N Santiago de Cuba, 1 (AMNH 89531).

Anolis e. palardis (3): Río Yateras, 5 mi. N river mouth, 1 (CM 333200); Baitiquirí, 1 (MCZ 42551); Guantánamo (U.S. Naval Base), 1 (MCZ 68921).

Anolis e. baracoae (6): Joar, Baracoa, 1 (MCZ 47050); Baracoa, 5 (AMNH 83628-30; MCZ 57404; MCZ 42520).

Anolis e. saxuliceps (4): Moa, 3 (HM 5376(2); HM 5374); *ca.* 7 km E Moa, 1 (MCZ 59324).

Anolis equestris incertae sedis: Santiago de Cuba (USNM 58855); coast south Pico Turquino (MCZ 42480); nr. Guantánamo (MCZ 8977); Guantánamo (USNM 58057; MCZ 57928); Imías (MCZ 42552); 8 mi. NE Felicidad (AMNH 83631).

LITERATURE CITED

BARBOUR, THOMAS, AND BENJAMIN SHREVE

1935. Notes on Cuban anoles. Occ. Papers Boston Soc. Nat. Hist., **8**:249-253.

HARDY, JERRY D., JR.

1958. A new lizard of the genus *Leiocephalus* from Cuba (Squamata: Iguanidae). Jour. Washington Acad. Sci., **48**(9):294-300, 5 figs.

MAERZ, A., AND M. REA PAUL

1950. A dictionary of color. New York, McGraw-Hill Book Co., pp. i-vii, 1-23, 137-208, 56 pls.

MARRERO, LEVI

1951. Geografía de Cuba. Habana, Alfa, pp. i-xvi, 1-736, 478 figs.

SCHWARTZ, ALBERT

1958. A new subspecies of *Anolis equestris* from eastern Cuba. Herpetologica, **14**(1):1-7, 1 fig.

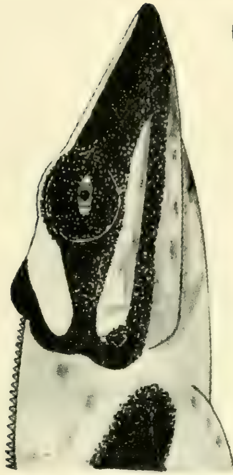
1960. Variation in the Cuban lizard *Leiocephalus raviceps* Cope. Proc. Biol. Soc. Washington, **73**:67-82, 10 figs.

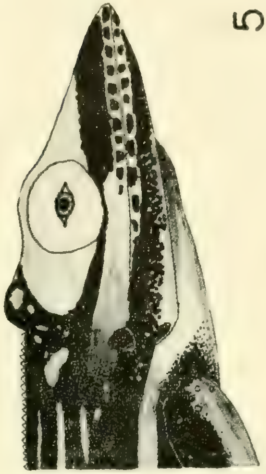
STEJNEGER, LEONHARD

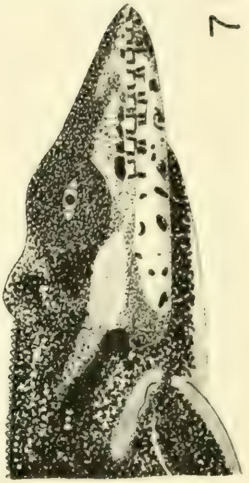
1917. Cuban amphibians and reptiles collected for the United States National Museum from 1899 to 1902. Proc. U.S. Nat. Mus., **53**:259-291, 128 figs.

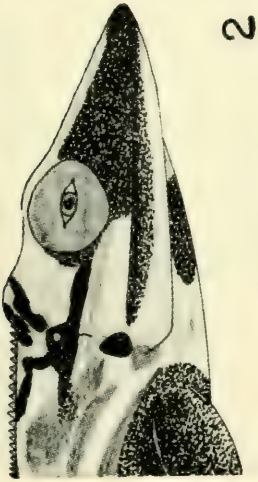
PLATE

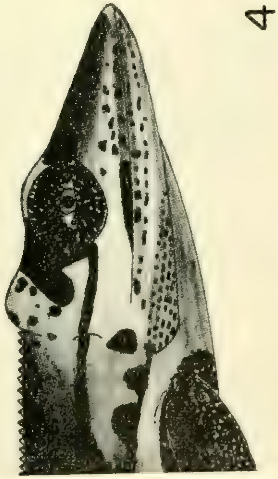
Figures 2-7. Lateral, semidiagrammatic, views of heads of six subspecies of *Anolis equestris* **from Oriente as follows:** Fig. 2, *noblei* (MCZ 26653, type). Fig. 3, *galeifer* (MCZ 59326, type). **Fig. 4,** *smallwoodi* (AMNH 89526, type). Fig. 5, *palardis* (CM 33320, type). Fig. 6, *baracoae* **(MCZ 57404, type).** Fig. 7, *saxuliceps* (HM 5376, type).

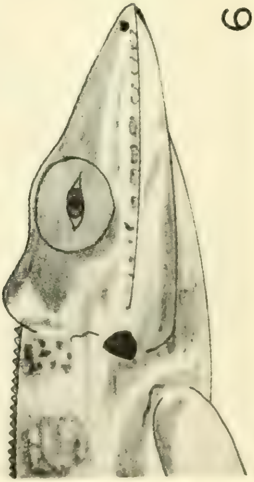

3


5


7


2


4


6

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 13

THE LYNX SPIDERS OF NORTH AMERICA, NORTH OF MEXICO (ARANEAE: OXYOPIDAE)

By Allen R. Brady

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
September 30, 1964

PUBLICATIONS ISSUED BY OR IN CONNECTION WITH THE

MUSEUM OF COMPARATIVE ZOOLOGY

HARVARD UNIVERSITY

BULLETIN (octavo) 1863 — The current volume is Vol. 131.

BREVIORA (octavo) 1952 — No. 207 is current.

MEMOIRS (quarto) 1864–1938 — Publication terminated with Vol. 55.

JOHNSONIA (quarto) 1941 — A publication of the Department of Mollusks. Vol. 4, no. 41 is current.

OCCASIONAL PAPERS OF THE DEPARTMENT OF MOLLUSKS (octavo) 1945 — Vol. 2, no. 28 is current.

PROCEEDINGS OF THE NEW ENGLAND ZOOLOGICAL CLUB (octavo) 1899–1948 — Published in connection with the Museum. Publication terminated with Vol. 24.

The continuing publications are issued at irregular intervals in numbers which may be purchased separately. Prices and lists may be obtained from the Publications Office of the Museum of Comparative Zoology, Cambridge 38, Massachusetts.

Peters' Check-List of Birds of the World. Volumes 1, 4 and 6 are out of print; volumes 2, 3, 5, 7, 9, 10 and 15 are currently available.

Phylogeny and Evolution of Crustacea. Proceedings of a conference held at Cambridge, Mass., March 6-8, 1962. H. B. Whittington and W. D. I. Rolfe, editors. Cambridge, Mass., 192 pp., 80 figs., 1963. Cloth bound, $6.75.

Fishes of the Gulf of Maine, by Henry B. Bigelow and William C. Schroeder. Washington, viii - 577 pp., 1953. Photo-offset reprint, $6.50.

PUBLICATIONS OF THE BOSTON SOCIETY OF NATURAL HISTORY

The remaining stock of the scientific periodicals of the Boston Society of Natural History has been transferred to the Museum of Comparative Zoology for distribution. Prices for individual numbers may be had upon request.

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 131, No. 13

THE LYNX SPIDERS OF NORTH AMERICA, NORTH OF MEXICO (ARANEAE: OXYOPIDAE)

By Allen R. Brady

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
September, 1964

Bull. Mus. Comp. Zool., Harvard Univ., **131** (13):429-518 September 1964.

No. 13. — *THE LYNX SPIDERS OF NORTH AMERICA, NORTH OF MEXICO (ARANEAE: OXYOPIDAE)*[1]

By

ALLEN R. BRADY

CONTENTS

Page
Introduction 432
Genera of Oxyopidae 433
Superfamily Lycosoidea 435
Biology of the Oxyopidae 436
Acknowledgments 438
Walckenaerian Names 439
Methods 442
Taxonomic Section
  Oxyopidae Thorell 444
  Key to Genera 446
  Oxyopes Latreille 447
  Species Groups of *Oxyopes* 448
  Key to Species of *Oxyopes* — Males 452
  Key to Species of *Oxyopes* — Females 453
    Oxyopes acleistus Chamberlin 454
    Oxyopes aureus sp. n. 457
    Oxyopes aglossus Chamberlin 461
    Oxyopes occidens sp. n. 464
    Oxyopes apollo sp. n. 467
    Oxyopes floridanus sp. n. 469
    Oxyopes tridens sp. n. 472
    Oxyopes pardus sp. n. 474
    Oxyopes lynx sp. n. 475
    Oxyopes felinus sp. n. 476
    Oxyopes salticus Hentz 478
    Oxyopes scalaris Hentz 484
  Hamataliwa Keyserling 496
    Hamataliwa helia (Chamberlin) 497
    Hamataliwa unca sp. n. 499
    Hamataliwa grisea Keyserling 501
  Peucetia Thorell 505
    Peucetia viridans (Hentz) 506
    Peucetia longipalpis F.O.P.-Cambridge 512
List of Collectors 515
Literature Cited 516

---

[1] This study was presented to the Department of Biology at Harvard University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

INTRODUCTION

The family Oxyopidae comprises 371[2] described species distributed chiefly throughout the tropical and subtropical regions of the world. This investigation is concerned with the evolutionary relationships and distribution of those species occurring north of Mexico. Of the 17 species involved, most occur only in the southern United States, but several occur over wide areas in the temperate and colder regions of North America. *Oxyopes salticus* and *O. scalaris* are found from coast to coast, and *O. scalaris* ranges from British Columbia and Labrador to northern Mexico. It is of interest that several widely distributed species of *Oxyopes* are also found in the temperate regions of Europe and Asia.

Large collections from Central America, Mexico and the West Indies were examined to determine the range of the oxyopids found north of Mexico. This study also illuminated the relationship between the Mexican, Central American and West Indian faunas and that of temperate North America. A preliminary examination of the species occurring in the Neotropical region reveals that the number of described species of Oxyopidae will almost certainly be doubled when the tropical regions have been fully investigated.

The oxyopid types of O. Pickard-Cambridge and F. O. Pickard-Cambridge (1894, 1902), deposited in the British Museum (Natural History), were examined as a part of this study. Their examination provided the information that determined whether or not the names used by O. P.- and F. O. P.-Cambridge should be applied to any of the oxyopids found north of Mexico.

C. A. Walckenaer (1838, 1841) in his ''Histoire Naturelle des Insects'' described six species of Oxyopidae from the Georgia region of the United States. These descriptions were based on the drawings in the unique manuscript of John Abbot (1792). The drawings are expertly done and adequate for identification of some species. However, it is often difficult or impossible to decide on the basis of color pattern what species is figured, and only if the specimen were at hand, or the genitalia figured, could one make an accurate decision. Walckenaer had few specimens to guide him and frequently placed spiders in the wrong family, e.g. *Sphasus vittatus* Walckenaer is obviously a clubionid, not an oxyopid. The Abbot manuscript, also deposited in the British

---

[2] Based on latest records in the Zoological Record, vol. 98, sect. 12, 1961.

Museum (Natural History), was examined and the drawings photographed. These colored photographs are deposited in the Museum of Comparative Zoology. The names pertaining to the Oxyopidae that Walckenaer applied to the drawings of Abbot and Bosc (1800) are discussed below.

GENERA OF OXYOPIDAE

Eleven genera are placed in the Oxyopidae at present. The number of species and the geographical distribution of species are listed in Table I. This list, based on that of Roewer (1954), includes the species described through 1961. Of the eleven genera listed, I have examined representatives of five (*Oxyopes*, *Hamataliwa*, *Peucetia*, *Oxyopeidon*, and *Tapinillus*) in collections from the entire world, with particular attention to those species occurring in North America, Mexico, Central America and the West Indies. From this study I conclude that *Oxyopeidon* must be synonymized with *Hamataliwa*, as Bryant (1948) has already pointed out. The genus *Oxyopeidon* was differentiated from *Hamataliwa* by the position of the anterior median eyes (AME) and by the spacing of the posterior median eyes (PME). Not only do such differences occur between closely related species, but these differences in eye arrangement may occur between sexes of the same species. The genus *Hamataliwa* is, therefore, redefined. From the descriptions in the literature it is apparent that the genus *Laestrygones* Urquhart is not an an oxyopid and should be removed from the Oxyopidae, as has been done by Bryant (1933) and Forster (1955).

The descriptions of *Hostus paroculus* Simon and *Pseudohostus squamosus* Rainbow, the type species of monotypic genera, place them well within the range of variation found among species of *Oxyopes*. Simon (1898) places *Meguilla truncata* Thorell, another type species, in the genus *Hamataliwa* where it probably belongs. Remaining in the family Oxyopidae, then, are six valid genera: *Oxyopes*, *Peucetia*, *Hamataliwa*, *Tapinillus*, *Schaenosceles*, and *Tapponia*. *Laestrygones* should be removed from the Oxyopidae. *Oxyopeidon* most certainly and *Meguilla* probably should be synonymized with *Hamataliwa*. The monotypic genera *Hostus* and *Pseudohostus* are probably synonyms of *Oxyopes*.

The structure of the genitalia, particularly of the male palpus, serves as an accurate indicator of generic as well as specific relationships. The above conclusions regarding the placement of genera were based on characters of the genitalia together with general body form and color, and the relative length of the legs. The arrangement of the eyes and the width of the various eye rows prove useful in separating some genera (Tables II and III), but they were not used as the primary basis for establishing genera, as in the past. The examination of oxyopids from all parts of the world has indicated that the genus *Hamataliwa*,

TABLE I

GENERA OF OXYOPIDAE

Genus (Type-Species)	Author	Geographical Distribution	Number of Species
Hamataliwa (grisea)	Keyserling, 1887	Neotropical	14
Hostus (paroculus)	Simon, 1898	Madagascar	1
Laestrygones (albiceres)	Urquhart, 1894	New Zealand and Subantarctic Isls.	3
Meguilla (truncata)	Thorell, 1897	Indochina	1
Oxyopeidon (putum)	O. P.-Cambridge, 1894	Ethiopian	5
		Neotropical	24
Oxyopes (heterophthalmus)	Latreille, 1804	Palaearctic	19
		Ethiopian	93
		Oriental	45
		Malay Peninsula to New Guinea	1
		Australian	23
		Neotropical	47
		Nearctic	11
Peucetia (viridis)	Thorell, 1869	Palaearctic	5
		Ethiopian	25
		Oriental	4
		Australian	2
		Neotropical	22
		Neotropical and Nearctic	1
Pseudohostus (squamosus)	Rainbow, 1915	Australian	1
Schaenioscelis (elegans)	Simon, 1898	Neotropical	7
Tapinillus (longipes)	Simon, 1898	Neotropical	4
Tapponia (micans)	Simon, 1885	Malay Peninsula and East Indies	13
		Total	371

Based on Roewer (1954) with additions from the Zoölogical Record through vol. 98, sect. 12, 1961.

when properly diagnosed, will undoubtedly prove to have a distribution comparable to that of *Oxyopes* and *Peucetia*. It is also possible that the large genus *Oxyopes* may be found to consist of several distinct groups each deserving generic status.

SUPERFAMILY LYCOSOIDEA

The oxyopids are grouped with the Agelenidae, Lycosidae, Pisauridae and Senoculidae in the superfamily Lycosoidea by most araneologists. The Oxyopidae, in common with most members of these families, possess: eight eyes, three tarsal claws without claw tufts, three pairs of spinnerets, two lung books opening at the corners of the epigastric furrow, a single tracheal opening in front of the anterior spinnerets, and a rather large colulus. In addition, all members of this superfamily, with the exception of the Agelenidae, have the trochanters notched. The trochanters of pisaurids and lycosids are more deeply notched than in oxyopids, while most agelenids do not have notches, although some do, according to V. D. Roth (per. comm.).

The lynx spiders are a highly specialized group of the Lycosoidea; that is, they are probably more unlike the ancestral stock than any other family in this complex. The agelenids, lycosids and pisaurids are linked by intermediate forms, whereas it is difficult to find intermediates between the oxyopids and any of these three families. I am not familiar with the spiders of the family Senoculidae except by examination of preserved specimens. They also appear to be a very distinct group of the Lycosoidea, but some authors place them near the Oxyopidae (Simon, 1898). On the basis of morphological characters and reported habits, I can see no close affinities between the Oxyopidae and Senoculidae. Although the oxyopids form a distinct line of evolution, their affinities unmistakably lie with the lycosoids.

Unlike most other representatives of the families of the Lycosoidea, the Oxyopidae are most active during the day. Many species are found running swiftly or jumping with great agility among low shrubs and herbs. The North American oxyopids are easily recognized in the field by the presence of numerous large erect spines on the legs (Figs. 4, 49, 50, 121, 138) and by their quick darting movements and sudden leaps. The posterior legs are well developed, concomitant with their jumping ability. The habits of these spiders and their relatively keen eyesight have earned for them the name *lynx* spiders.

Under the microscope one can readily identify the lynx spiders by their peculiar hexagonal eye arrangement (Figs. 1-3, 108-111, 136, 137). The eye arrangement and the spines on the legs most readily separate the oxyopids from all other families of spiders. In addition, the lynx spider fixes its egg case to a twig or leaf and enmeshes it with a network of silk, or suspends it from a small limb or branch with a guy-line. The female always stands guard over the egg case until the young emerge. The nearest counterpart to this type of maternal behavior is found in some pisaurids that construct a so-called nursery web and remain near the egg case until the young spiderlings appear. In addition to this behavioral similarity, some tropical pisaurids, such as *Thanatidius*, with long thin legs and many spines, resemble *Peucetia* and *Tapinillus* in general structure. *Thanatidius* also inhabits tall grass and herbaceous vegetation as do many of the oxyopids. For these reasons I think that the nearest living relatives of the lynx spiders are among the Pisauridae.

BIOLOGY OF THE OXYOPIDAE

The Oxyopidae are diurnal hunting spiders. Most of the lynx spiders move actively about in search of prey. However, they often pause and assume a characteristic prey-catching posture to await their victim. *Hamataliwa* lies very still waiting in ambush for its prey, as do many crab spiders. The great majority of oxyopids live in tall grass, low shrubs and herbaceous vegetation. A few (*Hamataliwa*) are evidently arboreal in habits and some appear to run over the bare ground.

That relatively little is known concerning the biology of the Oxyopidae is due chiefly to the difficulty of observing these spiders in the field. Probably 95 per cent of the oxyopids collected are taken by sweeping; thus they are observed only when they appear in the sweep-net. Judging from their local abundance, the lynx spiders are among the major predators of insects occurring in low shrubs and herbaceous vegetation. Very few observations have been made on the feeding habits of the lynx spiders. Recent investigations by W. H. Whitcomb and associates (1963) have disclosed that the lynx spiders are important predators of crop-damaging insects. *Oxyopes salticus*, one of the most common spiders of the cotton fields in Arkansas, has been reported as the chief predator of the cotton boll worm. *Peucetia viridans* is also an important predator on insect pests of cotton fields. Although several species of *Oxyopes* have been recovered from the nest of the mud-dauber, *Sceliphron coementarium*, these oxyopids do not constitute a large part of the prey of this wasp.

Among thousands of specimens of oxyopids examined during this investigation only very rarely was an egg case found. In several hundred vials containing *Oxyopes salticus*, only two egg cases were discovered. These were roughly spherical and about 3.5 mm in diameter; one contained 55 spiderlings and the other 18-20 eggs, each a little less than 1 mm in diameter. The extreme rarity of oxyopid egg cases is probably due to the method of collecting these spiders. In sweeping the vegetation the spiders are dislodged, but the egg cases, firmly attached to the vegetation, are not. Egg cases of *Peucetia viridans*, a much larger and more conspicuous lynx spider than *Oxyopes salticus*, are encountered more frequently. These egg sacs are rounded, from 12-25 mm in diameter, flattened on one side, and, except in the Southwest, have pointed projections on the surface. The eggs are about 1.5 mm in diameter. The number of eggs in an egg case is dependent on many factors and for that reason is extremely variable. The contents of nine egg cases of *Peucetia viridans* ranged from 197 to 602 eggs. Often the chief factor in determining the number of eggs deposited is probably the size of the individual spider, larger spiders depositing more eggs than smaller ones of the same species. *Peucetia viridans*, the largest North American lynx spider, produces many more eggs than the much smaller species of *Oxyopes*.

The North American lynx spiders evidently have one generation per year and probably construct only one egg case. The adults of several species of *Oxyopes* appear first in late spring (May and early June) and are most abundant in July and August. Adult *Peucetia* appear later, in late July and August, and are most abundant in August and September. In general there seems to be a correlation between the size of the species and its date of maturity. Smaller species of *Oxyopes* appear as adults in May, while *Peucetia* reaches maturity in July. From the limited information and observations made, it appears that most lynx spiders over-winter in the egg case as embryos or first instar spiderlings; however, in the extreme southern portions of their ranges there are probably several generations per year and adults may be found at any season.

Although very few observations have been made of oxyopids ballooning, they undoubtedly employ this means of dispersal. Glick (1939), in his study of the distribution of insects, spiders and mites in the air, reported 21 specimens of *Oxyopes* and one

Peucetia taken from 200-3,000 feet (70-1000 m), most nearer the lower elevation. These 22 specimens were collected from August, 1926 to October, 1931, in the air over Tallulah, Louisiana.

Suzuki (1952) reported that the chromosomes of five species of *Oxyopes* had been studied. All five species had 11 chromosomes in the haploid state and an XO sex-determining mechanism. The XO-mechanism of the male ($2N = 21$), as well as the number of chromosomes, was similar to that found in the subfamily Misumeninae of the family Thomisidae. In one species of *Peucetia* studied by Suzuki there were 13 autosomes and 2 X-chromosomes of different size. The male of *Peucetia* ($2N = 28$) was similar in these characters to many *Philodromus* species, as well as to most species of Lycosidae that were studied.

Since the oxyopids are diurnal and possess relatively keen sight, their courtship behavior probably plays an important role as a primary isolating mechanism. Mating in the Oxyopidae, however, has been observed only rarely, and the comparative aspects of this behavior are unknown. Gerhardt (1928, 1933) has observed courtship behavior in two European lynx spiders, *Oxyopes ramosus* and *Oxyopes heterophthalmus*. Although males of *O. heterophthalmus* readily displayed, Gerhardt (1933) succeeded in mating these spiders in captivity only once. Copulation is in the modified running-spider position (see Kaston, 1948, fig. 2006). The male approaches the female from in front and climbs on top. The venter of the female is slightly turned toward one side, allowing insertion of the palpus. In *O. heterophthalmus* the large tibial process (Fig. 101) of the male is used to orient the palpus. The male swings itself around 180° so that its body is in the same direction as the female's. No observations of the mating behavior of North American oxyopids have been recorded. A comparison of courtship behavior in the lynx spiders would, undoubtedly, prove most informative.

ACKNOWLEDGMENTS

I am greatly indebted to Dr. H. W. Levi of the Museum of Comparative Zoology, who, by his helpful advice, useful suggestions and constant encouragement, has made the preparation of this paper a much easier task. The collections of the Museum of Comparative Zoology and the library of this institution were invaluable to me during this investigation. I wish to thank sincerely Dr. W. J. Gertsch who placed the very large collections of the American Museum of Natural History at my disposal, thus making possible a thorough and complete analysis of many species. Dr. Gertsch was kind enough to include specimens that he had previously recognized as new species and they are described in this study with his permission.

During the course of this investigation I spent several weeks at the British Museum (Natural History) where I examined the types of O. P.- and F. O. P.-Cambridge. Photographs were also made of the plates of John Abbot (1792) which are deposited in the library of that museum. I am grateful to Dr. G. Owen Evans, Mr. Douglas Clark and Mr. Keith Hyatt for making my visit to the British Museum (Natural History) a most pleasant and profitable one. Professor M. Vachon supplied photographs of the Bosc plates, which are kept in the library of the Muséum National d'Histoire Naturelle, Paris.

A travel grant provided by the Evolutionary Biology Committee of the Biology Department of Harvard University made the trip to the British Museum (Natural History) possible. I wish to thank the Biology Department of Harvard University also for financial aid on several collecting trips into the southern United States.

Collections of Mrs. D. L. Frizzell (Dr. H. Exline) and Mr. J. A. Beatty aided me in this study considerably and I appreciate their loans in behalf of this investigation.

To the following persons and their respective institutions I wish to express my thanks for supplying regional collections that provided a more complete picture of the geographical distribution of certain species: Dr. H. K. Wallace, University of Florida; Mr. Vincent D. Roth, Southwestern Research Station; Dr. F. G. Werner, University of Arizona; Dr. George Byers, University of Kansas; Miss Beatrice Vogel, University of Colorado Museum; and Dr. C. A. Triplehorn, Ohio State University.

A special debt of gratitude is owed to Mrs. Lorna Levi for critically examining and editing the rough draft of this manuscript. Miss Susan Koelle mapped the species distributions and constructed the Dice-Leraas diagrams. National Institutes of Health grant AI-01944 helped defray some expenses involved in this study.

WALCKENAERIAN NAMES

Walckenaer (1838) in Volume I of "Histoire Naturelle des Insectes Aptères," named and described, from the Georgia region of North America, three new species of oxyopids in the genus *Sphasus*, a genus since synonymized with *Oxyopes*. In addition, Walckenaer (1838, 1841) named and described three species of *Clastes*, placed in the family Sparassidae, from the Georgia region. The six names that concern us in this paper were applied to the original drawings of the unique manuscript of John Abbot (1792). Since they were rediscovered in the British Museum (Natural History) by McCook (1888), the Abbot drawings have been considered the types of the Walckenaerian names by most North American araneologists. They had been used with some reservation, however, until Chamberlin and Ivie (1944) attempted ''to determine, as far as possible from available evidence, the proper application of the names based by Walckenaer upon Abbot's drawings of the spiders of Georgia.'' In their paper, Chamberlin and Ivie placed in synonymy many well-established names that had been used for North American spiders. Involved are 282 names that Walckenaer applied to drawings made by Abbot. These must be considered when revising almost any family of North American spiders. I agree with Levi and Levi (1961) that these names can only be given proper treatment by the investigator who has made a thorough and intensive taxonomic study of the spider genera in question. Unfortunately, Walckenaer made many mistakes in the identification of the Abbot drawings, and Chamberlin and Ivie have made some errors in their all-inclusive determinations of the Abbot drawings. A few of these errors are pointed out by Levi and Levi (1961) and this investigation has disclosed several more.

Of the three species of *Sphasus* (= *Oxyopes*) described by Walckenaer, only one appears to be an oxyopid. The disposition of the three is as follows:

Sphasus arcuatus Walckenaer (Abbot numbers 322, 323) is not an *Oxyopes*, as it was designated by Chamberlin and Ivie (1944), but probably belongs in the theridiid genus *Spintharus*. There are no spines on the legs of this spider as figured by Abbot, an important characteristic of all oxyopids; the color pattern is not like that of any oxyopid that I have seen, but is similar to that of *Spintharus flavidus* (Hentz); and the eye arrangement, a very important character, is not as in the Oxyopidae. Body form, coloration, and relative length of the legs is like that in *Spintharus flavidus* (Hentz).

Sphasus vittatus Walckenaer (Abbot number 369) is obviously not an oxyopid. This spider was placed in the genus *Castianeira* of the family Clubionidae by Chamberlin and Ivie

(1944). Judging from the original figure of Abbot, that is where it probably belongs. However, no species is known to which the description and figure can be applied.

Sphasus lanceolatus Walckenaer (Abbot number 42) is an oxyopid. Chamberlin and Ivie (1944) described a species of *Oxyopes* under this name. Although they designated a neotype, it has no validity since the holotype, namely Abbot's figure 42, is still extant. The neotype has since been misplaced or lost and was not available for examination; thus it cannot be compared with Abbot's original figure. We have only the figure of Abbot to guide us, and the dorsal view, showing the color pattern and eye arrangement, is not sufficient for diagnosis in this case. The colored drawing of Abbot, much like that of *Oxyopes scalaris* Hentz, may also be *O. aglossus* Chamberlin or *O. acleistus* Chamberlin. Chamberlin and Ivie (1944), however, considered these three species distinct from *O. lanceolatus*. *Oxyopes lanceolatus* has been perpetuated in the catalogues of Marx (1890), Petrunkevitch (1911), Roewer (1954), and Bonnet (1958). It has not otherwise been used in the literature except by Chamberlin and Ivie (1944). Since the name *O. lanceolatus* might be applied to at least four distinct species, I think that it is best considered a *nomen dubium*.

Three names proposed by Walckenaer (1838, 1841), *Clastes abboti* (Abbot number 401), *C. roseus* (Abbot number 411), and *C. viridis* (Abbot number 406), were recognized as the same species by Chamberlin and Ivie (1944). They applied the name *Peucetia abboti* (Walckenaer) to this large green lynx spider of the southeastern United States. The name *Peucetia viridans* (Hentz) had been used for this species for 100 years prior to the change by Chamberlin and Ivie (1944). Hentz's name actually has priority, having been used first in 1832, six years before Walckenaer's publication.

Walckenaer previously (1805) described and named another oxyopid for a drawing appearing in the unique manuscript of Bosc (1800) on the spiders of the Carolinas. This manuscript is deposited in the Paris Museum. The drawing (Bosc, pl. 4, fig. 1) was designated *Aranea fossana* by Bosc (1800), and its description was published by Walckenaer (1805) who called it *Sphasus fossanus*. Judging by Bosc's drawing and the description of Walckenaer, this species is *Peucetia viridans* (Hentz). *Oxyopa fossana* was listed by Simon (1864) and the name *Oxyopes fossanus* has been perpetuated in the catalogues of Marx (1890), Petrunkevitch (1911), Roewer (1954) and Bonnet (1958). The name has never been applied or used in any manner to designate a species of Oxyopidae. It is here considered a *nomen oblitum.*

In summary, the following dispositions have been made of the Walckenaerian names: *Sphasus arcuatus* is probably *Spintharus flavidus* Hentz; *Sphasus vittatus* is probably a *Castianeira; Sphasus lanceolatus* is a species of *Oxyopes,* but there is some doubt as to which one; *Clastes abboti, C. roseus,* and *C. viridis* are *Peucetia viridans* (Hentz). *Sphasus fossanus* is probably *Peucetia viridans* (Hentz), and is considered a *nomen oblitum.*

METHODS

Measurements. Two sets of oculars with accompanying grids were used in combination with low and high power objectives for making measurements. The higher power combination was used in measuring the width of the eye rows and was determined to be accurate to 0.0125 mm or one-tenth unit of the micrometer grid. The lower power combination was used to measure the body dimensions and leg lengths and was determined to be accurate to 0.1 mm or one-tenth unit of the micrometer grid. A measurement when retaken was nearly always read within one unit of the original measurement with either of the above micrometer grids, e.g. an original measurement of 7.5 micrometer units when retaken yielded 7.4-7.6 units. In all cases the greatest dimension of the structure was recorded, e.g. patella-tibia length was measured as the greatest distance from a line tangent to the most proximal part of the patella to a line tangent to the most distal part of the tibia. All available specimens of sparsely collected species were measured and a set of 30 specimens of each sex was measured for those species abundantly represented in collections.

A series of 15 measurements involving various components of the spider was made for each specimen. The range and mean of the total length for each species is given in its description and the relative length of the legs is also given. Other diagnostic measurements are recorded for *Oxyopes* in Table II and for *Hamataliwa* and *Peucetia* in Table III. The segments of leg I were measured from the prolateral aspect, as was patella-tibia II. The patellae-tibiae of legs III and IV were measured from their retrolateral aspect.

Figures and color descriptions. The color descriptions and illustrations are based on fresh alcoholic specimens in most cases and represent these species as they appear in nature. The genus *Peucetia* is an exception. This spider is bright green in life, but the color washes out rapidly in alcohol. Therefore, an attempt was made to describe both preserved and living animals of *Peucetia.*

Color descriptions and illustrations were made under low power (15X) of a dissecting microscope, with the spider illuminated by a microscope lamp. The well-marked specimens are those in which the hairs forming the color pattern have not been rubbed off. Where variation is great, the color pattern or patterns representative of the greatest number of specimens is described, with significant differences noted. Well-preserved alcoholic specimens of *Oxyopes* and *Hamataliwa* are very similar in coloration to the living spider. The most frequent differences are caused by shrinking in alcohol, which disrupts the pattern on the abdomen, and rubbing off of the spatulate appressed hairs that make up much of the color pattern in these two genera.

For each species the face view as well as the dorsal view of a male and female (when available) was drawn, with additional drawings to indicate variation. At least two drawings of the female genitalia were made for each species: a ventral external view of the epigynum after all the hair had been removed (often revealing some internal structure through the integument), and a dorsal internal view with the separated genitalia submerged in clove oil for clearing. The female genitalia of all species of *Oxyopes* and *Hamataliwa* are drawn to the same scale. *Peucetia* is drawn on a smaller scale. The scales are indicated on the plates. Two views of the male palpi were drawn for each species: a ventral view and a retrolateral view. The left palpi of the males were drawn after gently scraping them free of hair to reveal the palpal sclerites and the tibial and patellar apophyses. No attempt was made to indicate hirsuteness or spination in these drawings. All palpi of *Oxyopes* and *Hamataliwa* are drawn to the same scale. *Peucetia* palpi are drawn on a smaller scale.

That area referred to as the *face* is, in oxyopids, the anterior vertical plane of the head as seen from in front (Figs. 1 and 5). It comprises the frontal aspect of the carapace and includes the front of the chelicerae.

Records. Complete records for all the specimens examined during this investigation are listed in the Doctoral Dissertation. Copies of the dissertation are deposited in the library of the Biological Laboratories and in Widener Library, Harvard University. Locality records are listed geographically by states in a sequence from north to south and from east to west. Counties are listed alphabetically under states, cities and towns alphabetically under counties. Counties only are listed when a particular species is abundantly represented and obviously common in a given geographic area. For less well collected species full information is provided. The number of specimens collected at each locality is indicated, with the lower case ''o'' representing immature specimens in the same manner that the ♂ and ♀ signs represent the mature sexes. Collectors' initials, following the localities, are listed in a separate index at the rear of this paper. Occasional collectors are given by name.

TAXONOMIC SECTION

Family OXYOPIDAE Thorell

Oxyopidae Thorell, 1870, Nova Acta, Reg. Soc. Sci. Uppsala, Stockholm, 7(3):188, 196. Type-genus *Oxyopes*[3] Latreille, 1804.

Characteristics. Eyes: Anterior row recurved, except in some *Hamataliwa.* Anterior median eyes (AME) smallest, much smaller than the anterior lateral eyes (ALE). Posterior row procurved (except in *Tapinillus*). Posterior median eyes (PME) equal in size to posterior lateral eyes (PLE); both pairs larger than the AME, but smaller than the ALE, which are the largest (Figs. 1-3, 108-111, 136, 137). The AME row is much the smallest in width, the ALE row is always larger than the AME row, and subequal to the PME row, except in *Peucetia, Tapinillus,* and some *Hamataliwa* (compare Table II with Table III). The PLE row is the widest.

The chelicerae are very long and tapering at the distal end, and the fangs are short. The base of the fang occupies most of the distal end of the chelicera. The cheliceral margins are short and armed with one tooth on each side of the anterior and posterior margins (*Oxyopes* and *Hamataliwa*) or without teeth (*Peucetia and Tapinillus*). The boss on the anterior lateral face of the chelicera is not so prominent as in agelenids, pisaurids and lycosids. The articular sockets of the chelicerae at the lower margins of the face are heavily sclerotized and darkly pigmented.

---

[3] According to Thorell (1869) *Oxyopes* is derived from the Greek and means sharp-eyed.

The cephalothorax is variable in shape. The drawings of *Oxyopes* (Figs. 2, 3, 6), *Peucetia* (Figs. 137, 142) and *Hamataliwa* (Figs. 109, 111, 114) indicate the form of the carapace from above. *Oxyopes* has the carapace high and convex, sloping sharply at the thoracic declivity and at the sides. The face is almost vertical. *Hamataliwa* has the carapace even higher in many species, more sharply vertical at the thoracic declivity and sides, but with the face sometimes sloping more gradually and not vertical, as illustrated in Figures 109 and 111. *Peucetia* has the carapace more flattened, not as convex as in *Oxyopes*, and tapering gradually to the sides. This genus is more lycosid in appearance than the others. The thoracic groove is prominent in *Peucetia*, and not deep, but also usually well marked in *Oxyopes* and *Hamataliwa*.

The labium is always longer than wide and the endites exceed greatly its length and converge in front of it (Figs. 10 and 139). The sternum is roughly heart-shaped or shield-shaped (Figs. 10 and 139), and tapers behind to a thin projection between the posterior coxae.

The abdomen is elongate, widest immediately behind the base and more or less sharply tapering behind. In *Oxyopes* it is ovoid or elliptical and tapers sharply behind; in *Hamataliwa*, truncate near the base and again tapering to a point; but in *Peucetia* the abdomen is somewhat cylindrical, more elongate than in the two preceding genera, and tapering more gradually to the spinnerets.

The abdomen is connected to the cephalothorax by a short pedicle, often visible from above. The superior lorum, usually visible from above, is composed of a single undivided sclerite. It is divided into two sclerites in the Lycosidae and Pisauridae.

The six spinnerets are terminal. The cylindrical anterior spinnerets consist of a relatively large basal segment and an abbreviated, almost ring-like, apical segment. The posterior spinnerets, also two-segmented, are about the same length as the anterior, but more slender in diameter, with the apical segment shorter than the basal one, but larger than the distal segment of the anterior spinnerets. The tiny middle spinnerets are well hidden in their position between and slightly forward of the posterior ones. The second segment of the posterior spinnerets is tapered on its inner surface where it is supplied with a number of rather large spigots (tiny finger-like projections that house the openings of the silk glands). A short obtuse colulus is present immediately in front of the anterior spinnerets. The anal tubercle is prominent, roughly triangular in shape, and subsegmented.

The long legs are of unequal length (Figs. 4, 49, 50, 121, 138). The relative length of the legs is useful in separating genera and species groups. The order of leg length may be I-II-IV-III, I-II=IV-III, I-II-III-IV or IV-I-II-III. The males have more elongate tarsi and metatarsi than the females and longer legs in relation to their body length (Tables II and III). The legs are armed with very long spines, one of the most conspicuous characteristics of the family (Figs. 4, 49, 50, 121, 138). The trochanters have a shallow, crescent-shaped depression on the ventral surface.

There are three tarsal claws, the superior pair largest and provided with many fine teeth, the single inferior claw very small, with two or three fine teeth.

The integument of most oxyopids is copiously supplied with flattened, appressed hairs of varying colors, but usually elliptical or spatulate in shape. There are also modified translucent, flattened hairs, very scale-like in appearance, that give off brilliant metallic hues of lavender, green and blue. The spatulate hairs often cover much of the body and create the characteristic color patterns of the species (particularly in the genus *Oxyopes*).

The structure of the genitalia has a definite pattern within each genus. The palpi and epigyna are of prime importance in determining generic as well as specific affinities. The different structural patterns are discussed under each genus.

KEY TO GENERA

1a. Posterior cheliceral margin without teeth; ALE row obviously wider than PME row; posterior eye row (PME and PLE) only slightly procurved (Figs. 137, 142). Living specimens of bright green color .... *Peucetia*

1b. Posterior cheliceral margin with a single tooth on each side; ALE row subequal to PME row (Figs. 2, 3) or PME much wider than ALE (Figs. 109, 111); posterior eye row (PME and PLE) strongly procurved (Figs. 2, 3, or Figs. 109, 111). Living specimens not green in color 2

2a. Distance between PME subequal to distance between PME and PLE on each side (Figs. 2, 3) 3
2b. Distance between PME much greater than distance from PME to PLE on each side (Figs. 109, 111) ....*Hamataliwa* (except *H. helia*)
3a. Leg IV robust, obviously longer than leg III. Order of leg length I-II-IV-III, I-II = IV-III or IV-I-II-III. . . . . . *Oxyopes*
3b. Leg IV small, subequal in size to leg III. Order of leg length I-II-III-IV . . . . *Hamataliwa helia*

OXYOPES Latreille

Oxyopes Latreille, 1804, Tableau methodique des Insectes, Nouveau Dict. Hist. Nat., Arachnides, 24:135. Type species by monotypy: *O. heterophthalmus* Latreille, 1804, *op. cit.*, 24:135.

Characteristics. Eyes: AME smallest; PME and PLE subequal in size, larger than AME, but slightly smaller than ALE. ALE largest.

Width of eye rows: AME row much the smallest; ALE row subequal to the PME row. PLE row much the widest (Table II).

Cephalothorax high and convex, the cephalic region sometimes slightly elevated, sloping sharply at the thoracic declivity and along the sides. The face is almost vertical.

Labium longer than wide (Fig. 10). Endites exceeding the length of labium and converging in front of it.

Abdomen elongate, widest immediately behind base and tapering to spinnerets.

Legs very long in comparison to body length and unequal in relative length (Table II). Legs with numerous stout spines. Order of leg length I-II-IV-III or I-II=IV-III (*acleistus* group, *O. salticus*, *O. scalaris*) and IV-I-II-III (*apollo* group). Patellae-tibiae longer than femora or metatarsi, except on leg IV in some cases, thereby serving as a good indicator of leg length.

Integument richly supplied with flattened spatulate-shaped hairs that provide contrasting color patterns over most of body.

In the ventral view of the left palpus of the male the *embolus* curves from the base along the mesal edge of the *cymbium*, and describes a clockwise arc. The distal end of the embolus rests on a well-developed *conductor* (at approximately one o'clock), characteristic in size and shape for each species. At the point where the embolus arises, there is usually a structure which I call the *lamellar apophysis*, also of characteristic form and size for each species (Fig. 36).

Females with the epigyna variable, but with the internal genitalia of rather simple structure and generally uniform throughout the genus. External openings of the epigynum leading to a pair of heavily sclerotized bulb-shaped *seminal receptacles.* From the dorsal side of the seminal receptacles, a pair of lightly sclerotized, almost invisible, fertilization ducts arise and continue ventrally around the posterior neck of these bulbs (Fig. 15).

SPECIES GROUPS OF OXYOPES

The genus *Oxyopes* in North America may be separated into several distinct species groups: the *acleistus* group containing four species, the *apollo* group containing six species, and two independent species, *O. salticus* and *O. scalaris.* The establishment of these groups is based on similarities in genitalia, body structure, color pattern, and the relative length of legs.

Acleistus group. In the *acleistus* group (*O. acleistus, O. aureus, O. aglossus, O. occidens*), the females have a broad, heavily sclerotized bar forming the epigynum and covering the openings of the seminal receptacles (Figs. 16, 20, 22, 24) or a less heavily sclerotized epigynum with an inverse T-shaped central opening as in Figures 14 and 19. The palpi of the males have well-developed retrolateral tibial apophyses (Figs. 34, 36, 38. 40). *Oxyopes acleistus, O. aureus* and *O. aglossus* have distinct black lines on the ventral surfaces of femora I, II and III. *Oxyopes occidens* is the most divergent member of this group. It does not have these black lines under the femora, but has the same general color pattern. The epigynum as well as the male palpus and relative length of the legs of *O. occidens* ally it to the *acleistus* group.

The lynx spiders of the *acleistus* group all have the first leg longest and well developed. The second leg is usually next in length, although the fourth leg may be almost as long and is always more robust than the second leg. The patellae-tibiae are always I-II-IV-III in order of length (Table II). Femora IV are always strongly developed and the metatarsi exceed the length of the patellae-tibiae on leg IV.

A comparison of the species in this group is provided in Diagram 3 and a comparison of the *acleistus* group to other species of *Oxyopes* is provided by Table II. *Oxyopes acleistus* and *O. aureus* are the two species most alike in the group. They are very similar in the form of genitalia and in coloration and are entirely allopatric in distribution. *Oxyopes acleistus,* however, appears to be consistently smaller than *O. aureus.* Other differences between these two species are noted under the diagnosis of *O. acleistus*. *Oxyopes aglossus* is partially sympatric with *O. aureus* (Map 1) and is definitely smaller in size (Table II). *Oxyopes aglossus* and *O. acleistus* are closer in size than *O. aureus* and *O. acleistus* and may exclude one another from their ranges (Map 1). Observing the distribution of these species, we may theorize that *O. aglossus* has provided a barrier to gene flow between *O. aureus* and *O. acleistus* and effectively isolated these two speices.

The following hypothesis of historical events might explain the present distributions of these three species. *Oxyopes aureus* and *O. acleistus* were once a continuous interbreeding population, distributed from Mexico along the Gulf Coast into Florida, and this hypothetic species reached as far north as Kansas, Missouri, Illinois and Indiana. This was during an interglacial period of a more warm and favorable climate. *Oxyopes aglossus* at this time was even more northerly in distribution, reaching southern Canada. It was excluded from the range of *O. aureus-acleistus*, the postulated species, because of its similar ecological requirements. Later in their history these three incipient species were forced to retreat southward. For our purposes we may think of their retreat as coinciding with the advance of the ice cap during the Pleistocene. *Oxyopes acleistus* retreated into peninsular Florida while *O. aureus* retreated to the southern tip of Texas and northern Mexico. The advancing glacier also forced *O. aglossus* southward and it occupied the regions along the Gulf Coast vacated by *O. aureus* and *O. acleistus*, forming an effective barrier to gene flow between these two species. In this case we have probable historical events explaining the present distribution of these three species.

The relationships of the four species of the *acleistus* group are summarized in the following diagram. This diagram is based primarily upon morphological characters, but also takes into account distribution.

The lines leading to *O. aglossus* and *O. occidens* could be drawn to the right of *O. acleistus* and *O. aureus* as well as to the left, indicating equal similarity to both of these species. *Oxyopes occidens* is somewhat closer to *O. aglossus* in genitalia, but resembles *O. aureus* more in size and coloration.

Apollo group. The *apollo* group constitutes another complex of species recognized by their color pattern, all having the fourth leg longest and the palpus of the males with a well-developed apophysis on the patella, with the one exception of *O. felinus*.

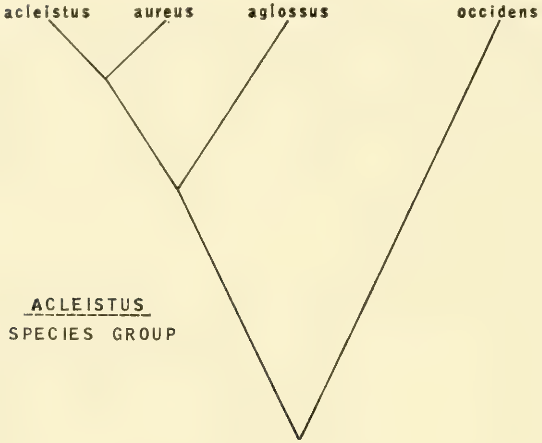


Diagram 1

In addition, the epigyna of the females that are known have a heavily sclerotized posterior rim in the shape of a crescent or bow as in Figures 47, 51, 53, 54. This species group consists of *O. apollo* and *O. floridanus,* two closely related species in the East, and *O. tridens, O. pardus, O. lynx,* and *O. felinus,* all found in the southwestern United States.

A comparison of the species in this group is provided in Diagram 4 and a comparison of the *apollo* group to other species of *Oxyopes* is supplied by Table II. Only three species were abundant enough in collections to construct Dice-Leraas graphs in Diagram 4. These graphs indicate that *O. apollo* and *O. floridanus* are morphologically very similar. These two species are separated primarily by differences in the male palpi and a greater abundance of spatulate hairs in *O. floridanus.* These slight differences are, however, indicative of reproductive isolation. The fact that *O. floridanus* is restricted to peninsular Florida serves to support its recognition as a separate species. Collections from intermediate geographic regions (Louisiana, Mississippi, Alabama, and western Florida) will help to determine if these two species, as I have called them, are reproductively isolated.

The western species of the *apollo* group, which we can define collectively as the *tridens* complex, are apparently all sympatric in a broad sense. They may be separated from one another altitudinally or by very restricted distributions within a geographic area, such as in mountain ranges (geographic isolation) or in certain habitats (ecological isolation). *Oxyopes tridens* seems to have a relatively wide distribution, however, being found at various altitudes and over a relatively wide geographic area. The reason for the extreme rareness of the other three species of the *tridens* complex (*O. lynx*, *O. pardus*, and *O. felinus*) may be attributed to their habits. All of the species of the *apollo* group are apparently ground inhabitants, that is, they run or hop about over bare ground. In the Southwest, *Oxyopes tridens* and related species have been collected as they jumped about on dry hillsides strewn with boulders and smaller rocks, but with very little vegetation. These species have been rarely taken by sweeping vegetation, but they may occur on certain types of plants when these are present.

It is significant to note that W. H. Whitcomb (pers. com.), who has collected extremely large numbers of *Oxyopes salticus* and a good number of specimens of *Oxyopes aglossus* by sweeping crop plants in Arkansas, has failed to collect even one specimen of *O. apollo* by this method. Instead, *O. apollo* is recovered rather frequently in pitfall traps laid flush with the ground.

The relationships of the six species that constitute the *apollo* species group are summarized in Diagram 2. This diagram is based primarily upon morphological similarities, but takes into account distribution as well. The male palpus of *O. felinus* does not have a patellar apophysis, but the color pattern, the structure of palpal sclerites and the long fourth leg places it near *O. tridens*, *O. pardus* and *O. lynx*. *Oxyopes apollo* and *O. floridanus* are obviously very similar to each other. *Oxyopes*

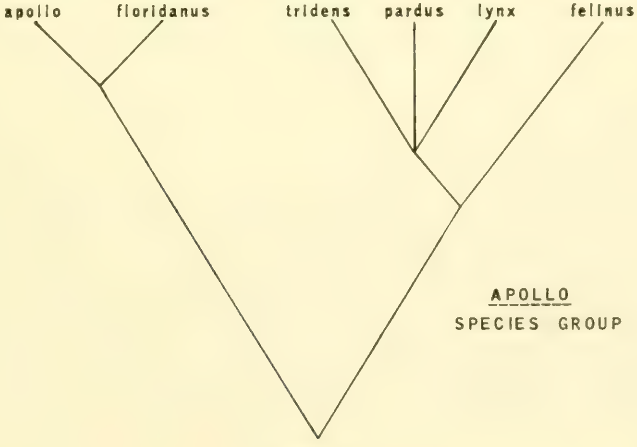


Diagram 2

tridens, *O. lynx* and *O. pardus* could be placed in any sequence, being equally alike or distinct. When the females of the latter two species and *O. felinus* are known, their relationships will become more clear.

The remaining two species of *Oxyopes*, *O. scalaris* and *O. salticus*, are very different from the other species north of Mexico and in their proper context would constitute separate species groups. *Oxyopes scalaris*, as has been pointed out, is similar to *O. ramosus* and *O. heterophthalmus* of Europe. Since *O. scalaris* is found as far north as Labrador we might hypothesize that the progenitors of this species came from the Eurasian continent by way of the British Isles, Iceland, and Greenland, to Canada where they occur today. Again, this migration must have occurred when the climate in these areas was warmer and more favorable. There are no oxyopids known from Iceland or Greenland at the present time.

Oxyopes salticus bears some resemblance to the four species in the *acleistus* group and might be placed with them in a subgeneric grouping. Comparison of *O. salticus* and *O. scalaris* with other species of *Oxyopes* can be seen in Diagrams 5 and 6. In Diagram 6, *O. apollo* and *O. tridens* have patella-tibia IV much longer than I. This trend in the *apollo* group, for the fourth patella-tibia to be longest, is evident in the figures in Table II and is correlated with the great length of the fourth pair of legs.

KEY TO SPECIES OF *OXYOPES*

MALES

1a. With distinct black lines on the ventral surfaces of femora I and II . 2

1b. Without distinct black lines on the ventral surfaces of femora I and II 5

2a. With a well-developed retrolateral tibial apophysis (Figs. 35-40) and no tuft or brush of stiff hairs on the ventral surface of the patella of the palpus. Color pattern as in Figures 27-32 3

2b. With the tibial apophysis concave, no well-developed retrolateral tibial apophysis, and with a tuft or brush of stiff hairs on the ventral surface of the patella of the palpus. Color pattern as in Figures 80-84. Palpus as in Figures 104, 105 . . . . *salticus*

3a. With two teeth at the base of the retrolateral tibial apophysis of the palpus (Figs. 35, 37) 4

3b. With only a single tooth at the base of the retrolateral tibial apophysis of the palpus (Fig. 39) . . . . *aglossus*

4a. Palpus with a large lamellar apophysis and tibial apophysis forming a less acute angle at the distal end (Figs. 35, 36). Texas and Louisiana .... *aureus*

4b. Palpus with a small lamellar apophysis and tibial apophysis forming a more acute angle at the distal end (Figs. 37, 38). Florida.... *acleistus*

5a. A conspicuous apophysis on the patella of the palpus and/or dorsal color pattern of longitudinal black and white stripes running the length of the body (Figs. 56-63). Leg IV longer than leg I 6

5b. Patella of palpus without apophysis and dorsal color pattern not black and white stripes running length of body. Leg I longer than leg IV 9

6a. Color pattern of longitudinal black and white stripes running length of body (Figs. 56-63) 7

6b. Color pattern not black and white stripes running length of body. Pattern as illustrated in Figures 72, 73 or 76, 77 8

7a. Palpus illustrated in Figures 70 and 71 .... *tridens*

7b. Palpus illustrated in Figures 68 and 69 .... *pardus*

7c. Palpus illustrated in Figures 66 and 67 .... *lynx*

7d. Palpus illustrated in Figures 64 and 65 .... *felinus*

8a. Palpus illustrated in Figures 74 and 75 .... *apollo*

8b. Palpus illustrated in Figures 78 and 79 .... *floridanus*

9a. Light yellow or golden in general appearance. Pattern illustrated in Figures 25 and 26. Palpus in Figures 33 and 34 .... *occidens*

9b. Russet brown, dark brown or gray in general appearance. Pattern illustrated in Figures 87 and 88. Palpus in Figures 106-107 .... *scalaris*

KEY TO SPECIES OF *OXYOPES*

FEMALES

1a. With distinct black lines on the ventral surfaces of femora I and II 2

1b. Without distinct black lines on the ventral surfaces of femora I and II 5

2a. Epigynum with an anteriorly directed scape (Figs. 91-96). Pattern illustrated in Figures 85 and 86 .... *salticus*

2b. Epigynum without an anteriorly directed scape; with a more or less well-developed posterior sclerotized rim or a heavily sclerotized transverse bar 3

3a. Epigynum consisting of a broad transverse bar (Fig. 22); pattern illustrated in Figures 9, 11, 12 .... *aglossus*

3b. Epigynum consisting of a sclerotized transverse posterior rim that has an anterior depression or with a less-heavily sclerotized transverse piece disclosing a central cavity (Figs. 14 and 16, 19 and 20) 4

4a. Central cavity of epigynum large, almost elliptical in shape (Fig. 19) or enclosed by a transverse sclerotized bar in which case the epigynum appears as in Figure 17 or 20. Florida .... *acleistus*

4b. Central cavity of epigynum narrow, inversely T-shaped (Fig. 14) or enclosed by a transverse sclerotized bar in which case the epigynum appears as in Figure 16 or 17. Louisiana and Texas .... *aureus*

5a. Leg IV longer than leg I 6
5b. Leg I longer than leg IV 8
6a. Color pattern of longitudinal black and white stripes extending length of body (Fig. 46); epigynum with strongly raised crescent-shaped posterior rim (Figs. 53 and 54) .... *tridens*
6b. Color pattern not of longitudinal black and white stripes, but as in Figure 42 or 44; epigynum with posterior rim only slightly raised (Figs. 47 and 51) 7
7a. Carapace, abdomen and legs heavily clothed with spatulate or elliptical-shaped, flattened white hairs. Florida .... *floridanus*
7b. Carapace mostly glabrous with scattered white hairs along vertical sides. Tennessee, Missouri, Arkansas, Louisiana, and westward . . *apollo*
8a. Russet brown, dark brown or gray in general appearance with contrasting white markings (Fig. 90); epigynum with an anteriorly directed scape (Figs. 98 and 99) .... *scalaris*
8b. Light yellow or golden in general appearance (Fig. 8); epigynum a transverse bar (Fig. 24) .... *occidens*

SPECIES DESCRIPTIONS

OXYOPES ACLEISTUS Chamberlin

Figures 5, 6, 18-20, 29, 30, 37, 38. Map 1.

Oxyopes acleistus Chamberlin, 1929, Ent. News, 40:19, fig. 3, ♀. Female holotype from Sanford, Seminole Co., Florida, in the American Museum of Natural History, examined. Roewer, 1954, Katalog der Araneae 2(a):330. Bonnet, 1958, Bibliographia Araneorum, 2(4):3223.

Oxyopes nelsoni Bryant, 1945, Psyche, 52(3-4):180, figs. 5, 7, ♂, ♀. Female holotype from Sebastian, Indian River Co., Florida, in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Discussion. The female described by Miss Bryant as *Oxyopes nelsoni* has a greater sclerotization of the epigynum, reducing the size of the central cavity that leads to the openings of the seminal receptacles (Fig. 20). The original description by R. V. Chamberlin was based on a specimen similar to Figure 19 in which the epigynum is less heavily sclerotized, and there is a characteristically shaped central cavity leading to the openings of the seminal receptacles. These two distinct forms of the epigynum are apparently characteristic of *O. acleistus*. Of the seven females of *O. acleistus* examined, two have the enclosed or "*nelsoni*" form of epigynum, three have the open or "*acleistus*" form of epigynum, and one is a bilateral combination similar to Figure 17. This dimorphism of the epigynum is found in the closely related species *O. aureus* in which both types occur in the same population as well as individuals that have one-half of the epigynum enclosed and one-half open. The male allotype of *O. nelsoni* from Sebastian, Florida, is identical with males of *O. acleistus*.

Structure. Length of seven females, 4.4-6.5 mm, mean 5.3 mm; length of nine males, 3.8-4.8 mm, mean 4.4 mm. Order of leg length I-II-IV-III. For comparison of certain diagnostic measurements of *O. acleistus* with those of other species see Table II and Diagram 3.

Color. Female. Pattern illustrated in Figures 5 and 6. Eyes circled with black, eye region dark brown, but heavily clothed with white hair. Face pale yellow to ivory. Vertical brown stripes beginning broadly under ALE, narrowing considerably at lower edge of clypeus and continuing to distal region of chelicerae. Carapace pale yellow to ivory with darker brown markings at anterior end. Wide dark brown submarginal stripes originating under PLE and continuing to posterior declivity. Thoracic groove a thin brown line. Darker patterns and stripes on carapace formed by tiny spatulate hairs.

Dorsum of abdomen pale yellow or cream colored from base to tip of spinnerets, bordered by dark brown or black. Two pairs of white indentations directed diagonally forward. Cardiac area slightly darker. Venter of abdomen pale yellow or cream with faintly indicated broad median stripe of darker brown, this stripe bordered by thin whitish lines. One specimen has the median stripe quite dark and distinct.

Legs pale yellow to ivory with longitudinal median black stripe on ventral surface of femora I, II and III. The black stripe is obsolete on leg IV, but may be represented by a series of dashes. The leg segments distal to the femora tend to be slightly darker and in some cases gray hairs form irregular dusky markings, particularly on the distal half of the femora. There may also be a slight green metallic sheen from the legs, although not so distinct as in the male.

Endites cream or ivory colored with black scopulae at inner margins of distal region. Labium slightly darker. Sternum ivory.

In some cases the spatulate hairs of the carapace may be rubbed off and the darker submarginal stripes are only faintly represented. Several of the specimens appear much lighter than in Figure 6 because the pale central area covers more of the dorsum of the abdomen and the marginal areas are not so dark and contrasting. They appear much the same as *O. aureus* in Figure 3.

Male. Pattern illustrated in Figures 29 and 30. Eyes circled in black with black bands extending from each eye toward center of eye hexagon. Face light brownish yellow or gold with vertical black lines extending from ALE to distal region of chelicerae, as in Figure 29, or with face mostly black, as in Figure 27. Eye region with iridescent scales particularly from ALE to PME. The palpi are velvety black, and in some specimens they exhibit a blue iridescence.

Carapace brownish yellow or golden with broad submarginal brown stripes as in female.

Dorsum of abdomen ranges from almost white to gray depending upon abundance of spatulate hairs. Sides of dorsum are gray to black. Dorsum with scattered iridescent scales. Venter of abdomen ranging from pale yellow with dusky median stripe to gray with a black median stripe outlined in yellow. Iridescent scales more numerous on venter than dorsum.

Legs yellow with black stripes on the ventral surfaces of femora I, II, and III. In most specimens the legs exhibit a green metallic sheen due to iridescent scales.

Endites pale yellow to brown with the distal ends lighter. Labium darker, brownish yellow to dark brown. Scopulae black. Sternum pale yellow or cream.

Diagnosis. Oxyopes acleistus is most similar to *O. aureus* in coloration and in the form of the male and female genitalia. A comparison of Figure 14 with Figure 19, however, reveals distinct differences between the central cavities of the epigyna. In the palpi the median apophysis of *O. acleistus* is smaller than in *O. aureus* (compare Fig. 38 with Fig. 36) and the tibial apophysis of *O. acleistus* forms a more acute angle toward its distal end than in *O. aureus* (compare Fig. 37 with Fig. 35).

Because *O. acleistus* and *O. aureus* are similar and occur as distinct allopatric populations, one might assume them to be subspecies (Map 1). However, in addition to the differences in genitalia already noted, a comparison of the diagnostic measurements in Table II and in Diagram 1 reveals that *O. aureus* is probably consistently larger than *O. acleistus.* All of these differences indicate that isolating mechanisms exist between the two, and that *O. acleistus* and *O. aureus* would not interbreed if they were to come into contact.

It is interesting that in many cases (Wallace, 1942a, 1942b; Brady, 1962; McCrone, 1963) the distribution of spider species found in Florida is restricted to the peninsula or does not extend far beyond the limits of the state. Almost any large revision will reveal cases of this limited distribution.

Natural history. Males and females of this species were collected by sweeping short grass and herbaceous vegetation. During early June they did not occur in great abundance and only a few specimens were captured in approximately two hours of sweeping. *Oxyopes aclcistus* seems to prefer low vegetation in shaded areas. A single male was found running over the outside wall of a tent at Gold Head Branch State Park and a female was taken from the top of a picnic table at the same location.

Distribution. Florida (Map 1).

Records. Florida. Dade Co.: ♂ (THH); Homestead ♀♀. Highlands Co.: Highlands Hammock St. Pk. near Sebring, 21 June 1962, ♂♂♀♀ (ARB, JAB). Indian River Co.: Sebastian, 1-8 Apr. 1944, ♂♂♀ (GN). Orange Co.: 10 mi. SW of Orlando, 23 Aug. 1944, ♂ (MN). Putnam Co.: Gold Head Branch St. Pk., 13 June 1962, ♀ (ARB), 14 June 1962, ♂ (C. Zeiger); Welaka, 21 June 1946, ♂♂ (R. E. Bellamy). Seminole Co.: Sanford, 27 July 1927, ♀ (Stone).

OXYOPES AUREUS sp. n.

Figures 1-4, 13-17, 27, 28, 35, 36. Map 1.

Holotype. Female from Bentsen State Park, 6 mi. SW of Mission, Hidalgo Co., Texas, 30 June 1962 (A. R. Brady) in the Museum of Comparative Zoology. The specific name is an adjective meaning golden.

Discussion. Oxyopes aureus is probably the most variable species of this genus in North America with regard to local populations. The female may appear dark with a distinct abdominal pattern (Fig. 1), or may appear much lighter (Fig. 3). In addition, the male may have the face lined with black (Fig. 29) or almost entirely black (Fig. 27). The female epigynum also shows considerable variation (Figs. 14-17). Of 30 females examined, 17 have the epigynum as in Figure 14, eight as in Figure 16, and five females have a bilaterally divided combination as in Figure 17. All three types of epigyna are encountered in the same local population.

Since there are two rather distinct epigyna (Figs. 14, 16) and two relatively distinct color patterns (Figs. 1, 3), it was thought that two species might be present. The correlation between color pattern and the type of epigynum was closely checked. Although many specimens with a color pattern as in Figure 1 had an epigynum as in Figure 16, and many specimens with a color pattern as in Figure 3 had an epigynum as in Figure 14, these combinations were not found in a number of individuals. Also the color patterns formed a continuum and in some cases were difficult to classify.

The size of the female specimens was also checked carefully with respect to the possession of a particular color pattern and/or a specific type of epigynum. Again there was no definite relationship. It appears that the variation in this species represents a case of genetic polymorphism and is not related to age or size, or caused by gravidity of the female.

That only one species is represented here seems certain if it is considered that: (1) all types of variants occur in local populations with no visible ecological differences, (2) internally the female genitalia are alike, (3) intermediates (Fig. 17) occur between epigynal types, and (4) there is only one male encountered, i.e. the male palpus shows no variation. The same kind of polymorphism that occurs in *O. aureus* is present in *O. acleistus* as well. Both species are extremely interesting because of this phenomenon and deserve further analysis, mainly because much of spider taxonomy in particular, and arthropod taxonomy in general, is based on the ''invariability'' of genitalic structure.

Structure. Length of 30 females, 5.0-7.3 mm, mean 6.0 mm; length of 26 males, 4.1-5.2 mm, mean 4.6 mm. Order of leg length I-II-IV-III. For comparison of certain diagnostic measurements of *O. aureus* with those of other species see Table II and Diagram 3.

Color. Female. Pattern variable, ranging from dark colored, well-marked individuals as in Figure 1 to lighter, less distinctly marked specimens as in Figure 3. Eye region dark brown, thickly clothed with white appressed hairs. Eyes circled in black with a black band running from each toward center of eye hexagon. Face pale yellow to cream or ivory. Vertical brown stripes beginning broadly under ALE, narrowing considerably at lower edge of clypeus and continuing to subdistal region of chelicerae.

Carapace cream colored to ivory. Wide submarginal stripes of brown spatulate hairs beginning below PLE and continuing posteriorly to thoracic declivity. Well-marked specimens have in addition dark markings behind the PME and surrounding the thoracic groove, produced by appressed spatulate hairs.

Dorsum of abdomen white to cream colored. In well-marked individuals, white overlaid with brownish yellow spatulate hairs produces a golden appearance. Cardiac region with lanceolate marking of slightly darker color, outlined in brown. Lanceolate mark absent in many pale specimens. Pale central region of dorsum more or less extensive (compare Fig. 1 with Fig. 3) and bordered by dark brown or black. Two pairs of pale lateral indentations on posterior half of abdomen, accented with white hairs and directed anteriorly. Venter of abdomen cream colored with median longitudinal brown stripe from epigastric furrow to spinnerets.

Legs ivory. Distinct black median longitudinal stripes on ventral surfaces of femora I, II, and usually III. Stripes less distinct on femur IV, sometimes absent. Dusky markings on legs, more pronounced on distal ends of femora, tibiae and distal segments. Legs duskier on well-marked specimens.

Endites ivory with dark sclerotized outside borders, black scopulae. Labium cream colored, sometimes with dusky clothing of fine hair making it darker. Sternum ivory, dusky around margin, with conspicuous black hairs.

Specimens marked as in Figure 1 are characterized by a much greater abundance of scale-like spatulate hairs (both light and dark) that form the type of pattern illustrated. When these are rubbed away the specimens tend to become lighter in appearance and more like Figure 3.

Male. Pattern illustrated in Figures 27 and 28. Eye region dark brown to black. No white hairs present. Iridescent spatulate hairs from ALE to AME. Palpi velvety black with metallic blue sheen. Face dark orange-brown with dusky markings as in Figure 29, to almost entirely black. Some specimens have a definite black reticulum and most of the face and chelicerae black (Fig. 27). Vertical black stripes are often indistinguishable, being completely obliterated by black color on the chelicerae as well as on the clypeus.

Carapace light yellow-orange or golden. Dusky submarginal stripes beginning under PLE, curving dorsally and continuing to posterior declivity of thoracic region *or* submarginal stripes absent with the carapace almost glabrous, having only a few scattered spatulate hairs.

Dorsum of abdomen with broad median area of ivory to cream, covered with grayish scales in greater or less abundance. Bordered on sides by dark gray-brown. Venter cream to pale yellow with broad median longitudinal gray-brown stripe from epigastric furrow to base of spinnerets or venter almost entirely black with median stripe bordered by a thin pale line. Black patch over genital area, lung book covers pale yellow or cream. Iridescent scales usually numerous on venter.

Legs ivory with distinct black stripes on ventral surface of femora I and II, but these stripes only faintly represented on femora III and IV. Scattered dusky markings, usually on dorsal surface of leg segments. Femora with faint green metallic luster.

Endites pale yellow to ivory with outer edges dark brown, sclerotized. Usually lighter in color at distal ends, with black scopulae. Labium darker, brownish. Sternum ivory to cream.

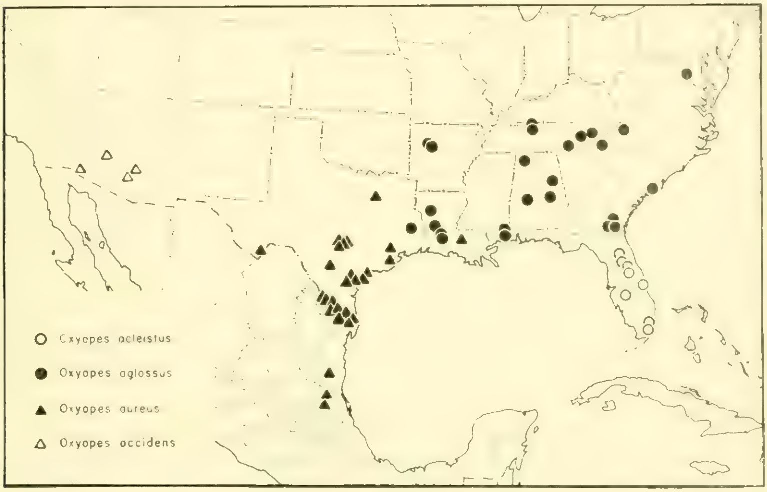
Diagnosis. Oxyopes aureus is most similar to *O. acleistus*, which it resembles in coloration and in genitalic structure. These two species can be best differentiated by comparing the epigynum of *O. aureus* (Fig. 14) with *O. acleistus* (Fig. 19). For other differences see the discussion under the diagnosis of *O. acleistus.*

Natural history. In southern Texas adult males of *O. aureus* first appear in April and have been collected through September. Females appear in May and may be found as late as November. Adult individuals are most abundant in late June and early July. *Oxyopes aureus* was collected by sweeping grass and other herbaceous vegetation at Corpus Christi State Park and Bentsen State Park in southern Texas. These spiders were most abundant in relatively short vegetation (6-8 inches) in shaded areas, particularly under the cover of trees. At Corpus Christi Park they occurred in close proximity to *O. salticus.* The latter species, however, was much more abundant in open unshaded areas and in taller grass along the lake shore. Nearly all of the specimens of *O. salticus* that were collected from 28 June-1 July at the above localities were immature. Mature males and females of *O. aureus* were relatively abundant during this same period. At Goose Island State Park *O. aureus* was collected in sweeping Compositae. This species has been found in mud-daubers' nests, but it is not taken in great numbers by these wasps.

Distribution. Louisiana, Texas, and Mexico (Map 1).

Records. Louisiana. East Baton Rouge Par.: Baton Rouge, June 1954, ♀ (NB). *Texas.* Aransas; Atacosa; Bee; Brazoria; Brewster; Calhoun; Cameron; Dallas; Harris; Hidalgo; San Patricio; Starr; Travis.

MEXICO. *Tamaulipas.* Rio Gualolejo near Forlon, 16 Apr. 1938, ♂ ♀ ♀ (LID, B. Brown). *San Luis Postosí.* Huichihuayan, 19 May 1952, ♂ (MAC, WJG, RS), 10 mi. N of Valles, 23 July 1945, ♂ (A. M. Dame).



Map 1

OXYOPES AGLOSSUS Chamberlin

Figures 9-12, 21, 22, 31, 32, 39, 40. Map 1.

Oxyopes aglossus Chamberlin, 1929, Ent. News, 40:17, figs. 1, 2, ♀, ♂. Female holotype from Billy's Island, Okefenokee Swamp, Georgia, in the American Museum of Natural History, examined. Roewer, 1954, Katalog der Araneae, 2(a):333. Bonnet, 1958, Bibliographia Araneorum, 2(4):3223.

Discussion. Oxyopes aglossus does not exhibit the polymorphism shown in *O. acleistus* and *O. aureus.* There is also little geographic variation in color over its entire range of distribution (see Map 1). The affinities of *O. aglossus* undoubtedly reside with *O. acleistus* and *O. aureus,* and it is considered to belong to the same species group.

Structure. Length of 30 females, 4.5 - 6.7 mm, mean 5.4 mm; length of 26 males, 3.9 - 4.8 mm, mean 4.4 mm. For comparison of certain diagnostic measurements of *O. aglossus* with those of other species see Table II and Diagram 3.

Color. Female. Pattern illustrated in Figures 9, 11 and 12. Eyes circled in black with black band leading from each eye toward center of eye hexagon. Eye region thickly clothed with white hair. Face cream to pale yellow. Black stripes beginning below AME and continuing to distal region of chelicerae.

Carapace cream to pale yellow. Wide brown submarginal stripes originating anteriorly below ALE and continuing to thoracic declivity. Often an irregular brown pattern behind PME and surrounding thoracic groove.

Dorsum of abdomen cream to pale yellow; often with white pigment underlying integument, pigment most conspicuous near anterior end of abdomen. Cardiac area pale, faintly outlined by darker brown spatulate hairs. Lateral areas brown or irregularly spotted with brown. Usually two pairs of indentations from pale central region into darker lateral areas are visible on posterior half. Venter of abdomen cream colored with broad median dark brown or black stripe from epigastric furrow to spinnerets.

Legs pale yellow. Ventral surfaces of femora I and II with black median longitudinal stripes; represented on femora III and IV only by a series of black dashes.

Endites pale yellow; sclerotized region around outer edges, brown. Labium pale yellow. Sternum cream to pale yellow.

Male. Pattern as illustrated in Figures 31 and 32. Eyes circled with black and with black bands extending toward center of eye hexagon. Iridescent scales from ALE to PME. Palpi black with iridescent blue sheen. Vertical black stripes from AME to distal region of chelicerae. Distal ends of chelicerae pale.

Carapace pale yellow-orange (golden) to brownish yellow. Broad dusky submarginal stripes. Vertical sides lighter in color than dorsal surface.

Dorsum of abdomen cream with lateral areas dark brown or almost black due to presence of dusky scales. Pink and lavender iridescence occurs wherever these gray scales are present, many times over entire dorsal surface. Venter with very wide dark brown to black stripe from epigastric furrow to spinnerets, bordered by pale lines. In some cases the entire ventral surface is dark gray-brown to black and heavily covered with scales. Genital region dusky with lung book covers pale.

Legs cream to yellow. Femora I and II with median ventral black stripe, stripes broken and indistinct on femora III and IV.

Endites cream to yellow with dusky markings along outer edges. Labium cream to brownish yellow. Sternum pale cream to yellow.

Diagnosis. Oxyopes aglossus is most similar to *O. acleistus* and *O. aureus*. The chief similarities are in general color pattern, relative length of the legs, and particularly the male palpi (Figs. 35-40). Females of *O. aglossus* are easily separated from *O. acleistus* and *O. aureus* by the form of the epigynum (compare Fig. 22 with Figs. 14, 16 and 19, 20). The differences in the male palpus are in the conductor, which is more square at the distal end in *O. aglossus* (compare Fig. 40 with Figs. 36 and 38), and in the tibial apophysis, which has only a single tooth at the base in *O. aglossus* as opposed to two teeth in *O. acleistus* and *O. aureus* (compare Fig. 39 with Figs. 35 and 37).

Natural history. I have not collected this species in the field. In habits it is probably similar to *O. aureus* and *O. acleistus*. Many specimens of *O. aglossus* were included in vials with *O. salticus* so that they must have similar habitat preferences, that is, grass and other herbaceous vegetation. A number of specimens are from relatively high elevations in Tennessee and North Carolina, but there are also specimens from localities near sea level in Mississippi. Several specimens were recovered from the nest of *Sceliphron*.

Distribution. Virginia, Tennessee, North Carolina, south to Alabama, Mississippi, Louisiana, and west to Texas.

Records. Virginia. Fairfax Co.: Great Falls, 21 June, ♀ (NB). *Tennessee.* Grundy Co.: Beersheeba, June 1888, ♂. Knox Co.: Univ. of Tennessee Farm, 3 June 1951 ♂, 6 June 1951, ♀ (H. B. Reed); Knoxville, 14 July, ♀ (W. B. Cartwright). Loudon Co.: Lenoir City, 20 July 1903, ♂ (JHE). Robertson Co.: Greenbrier, 16 June 1939, ♂ (DCL); 30 mi. N of Nashville, 16 July 1933, ♀ (WJG). *North Carolina.* Avery Co.: Pineola, 14 July 1903, ♂ (JHE). Durham Co.: Duke Forest, Durham, 13-18 June 1933, 3 ♂ ♂ :6 ♀ ♀ :o (AMC); 11-20 June 1953, ♂ o (HWL); 14 Sept.-11 Oct. 1935, ♀ (AMC). Orange Co.: Chapel Hill, July, ♂ (JHE). Transylvania Co.: Brevard, 3 July 1942, 3 ♂ ♂ : ♀ (Westfall). Wake Co.: Raleigh, May 1945, ♀, July 1912, ♀, 12 Aug. 1943, ♂ (CSB). *South Carolina.* Charleston Co.: McClellanville, July-Aug. 1945, ♀ (PV). Kershaw Co.: 4 mi. N of Cassatt, 12 June 1935, ♂ (WJG). *Georgia.* Okefenokee Swamp, Billy's Island, June 1912, ♂ ♀ ♀, Honey Island ♂ ♂, Mixson's Hammock, 16 June 1912, ♂ :4 ♀ ♀ (CRC). Ware Co.: Waycross, ♀. *Alabama.* Baldwin Co.: Silverhill, Apr.-May 1945, ♂, Aug. 1947, ♀ (GN). Clay Co.: Cheaha St. Pk., June

1940, ♂ (AFA). Lawrence Co.: Black Warrior Nat. Forest, June 1939, ♂ ♂ ♀ ♀ o (AFA). Tallapoosa Co.: Alexander City, 1-14 Aug. 1944, 3 ♀ ♀ (GN). Tuscaloosa Co.: Alberta City, June 1947, ♂ (AFA). *Mississippi.* George Co.: Lucedale, June 1932, ♂ ♀ (HD). Jackson Co.: 2-15 Sept. 1942, ♀ (BM). *Louisiana.* Grant Par.: Bayou Bouef, Bringhurst, 20 June 1941, ♂ (SEJ, AFA); State Forest, Woodworth, 21 June 1941, ♀ ♀, (SEJ, AFA). Winn Par.: Kisatche Forest, Winnfield, 13 July 1943, ♀. *Arkansas.* Conway Co.: 7 June 1962, ♂ (HEF), Plumerville, 12-18 June 1957, ♀ (L. Moore). *Texas.* Jasper Co.: 5 mi. N of Jasper, 6 June 1936, ♂ ♀ (SM).

OXYOPES OCCIDENS sp. n.

Figures 7, 8, 23-26, 33, 34. Map 1.

Holotype. Male from Sabino Pond, Sabino Canyon, Santa Catalina Mtns., Pima Co., Arizona, 10 July 1962 (A. R. Brady) in the Museum of Comparative Zoology. The specific name is a noun in apposition meaning the West.

Structure. Length of ten females, 5.5 - 8.4 mm, mean 6.9 mm; length of five males, 5.1 - 5.6 mm, mean 5.4 mm. Order of leg length I-II-IV-III. For comparison of certain diagnostic measurements of *O. occidens* with those of other species see Table II and Diagram 3.

Color. Female. Pattern illustrated in Figures 7 and 8. Eyes ringed with black and with black bands directed toward center of hexagonal eye region. Eye region black, heavily clothed with white hairs. Face ivory to pale yellow. Vertical black stripes beginning under AME and continuing to subdistal region of chelicerae. Chelicerae slightly darker in color, heavily sclerotized outer margins dark brown.

Carapace ivory to pale yellow. Wide brown submarginal stripes, originating anteriorly under PLE and continuing diagonally upward and posteriorly to thoracic declivity. Brown dashes behind PME and at thoracic groove.

Dorsum of abdomen cream to pale yellow produced by white overlaid with more or less dense clothing of brown, flattened, elliptically-shaped hairs. Darker brown marking indicating cardiac region. Lateral areas dark brown with color becoming darker posteriorly. Dark brown or black dashes outlining the median pale stripe at posterior end, with a pair of pale indentations just anterior to these. Venter of abdomen with broad median longitudinal stripe of light brown, outlined with white and the sides darker brown or area lateral to median dark stripe cream without darker markings.

Legs ivory to pale cream without any distinct darker markings. No black stripes on femora.

Endites pale cream to pale yellow with black scopulae at distal ends. Labium darker brown with reddish tinge. Sternum ivory to cream.

Male. Pattern illustrated in Figures 25 and 26. Eye region dark brown or black without white hairs. Iridescent scales over eye region producing a metallic lavender or green luster, most noticeable between ALE. Scales scattered over face as well. Palpi black, heavily clothed with long black hair.

Carapace cream to pale yellow with very light brown submarginal stripes formed by short hairs. Thoracic groove faintly indicated.

Dorsum of abdomen with median white area from base to spinnerets, giving off a pair of lateral white dashes posteriorly. Covered by very light brown spatulate hairs and scattered iridescent scales. Lanceolate mark of light brown in cardiac area. Venter with wide, brown, median longitudinal stripe, bordered by thin white lines on each side. Lateral area very light brown or tan.

Legs ivory to cream, without distinct darker markings.

Labium and endites cream with black scopulae at distal ends of endites. Sternum ivory.

Diagnosis. Oxyopes occidens is similar to *O. aglossus* and bears some resemblance to *O. aclcistus* and *O. aureus.* With these three species *O. occidens* constitutes what is termed in this paper the *aclcistus* species group. *Oxyopes occidens* is the largest and most divergent member of this group and also the lightest in color. It can be easily distinguished from the other members of the group by its color pattern(Figs. 7 and 8) and especially the male or female genitalia (Figs. 33, 34 or Figs. 25, 26). *Oxyopes occidens* is the only representative of this species complex in the western United States.

Natural history. This spider was collected from very dry, almost dead vegetation (primarily *Rumex* or ''Dock'' as it is commonly called) located near a pond. It exhibited excellent jumping ability, leaping among the dried stalks and leaves of *Rumex* when disturbed. This lynx spider could only be collected by quickly grabbing it with the hand. Sweeping of the vegetation did not yield a single specimen.

Distribution. Arizona (Map 1).

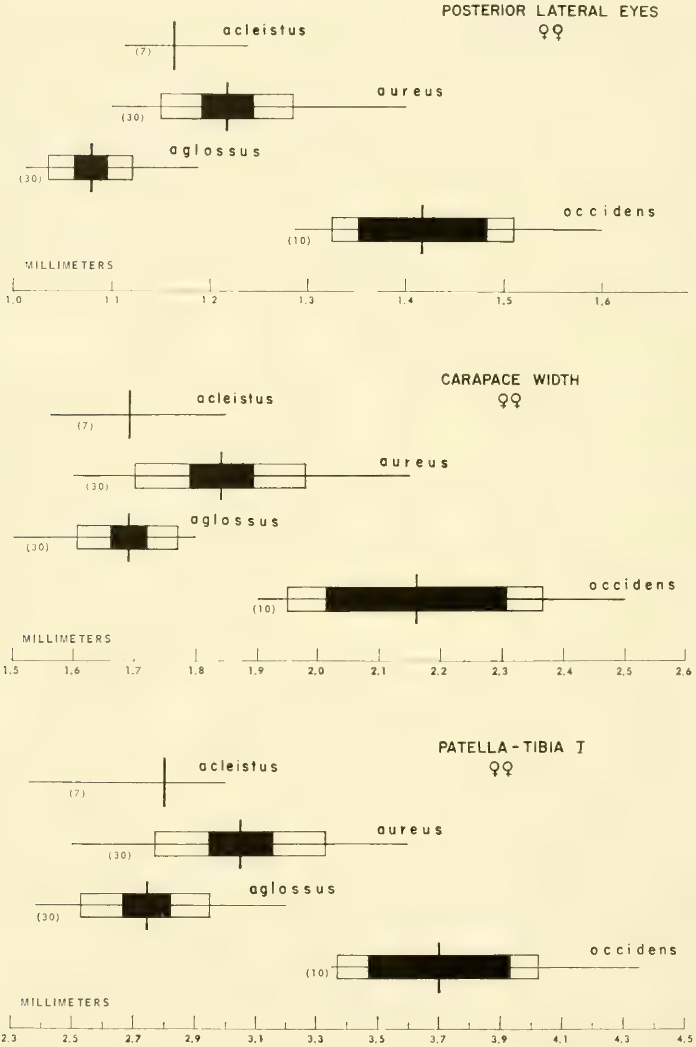


Diagram 3 — Measurements of the *Acleistus* Group.
Modified Dice-Leraas diagrams. The horizontal line represents the observed range, the open rectangle shows the standard deviation and the solid black rectangle indicates the 95 per cent confidence intervals for the mean. The mean is denoted by a vertical line and the number of specimens measured is given in parentheses.

Records. Arizona. Maricopa Co.: Phoenix, 17 Oct. 1960, ♀, (H. L. Stahnke). Pima Co.: Sabino Pond, Sabino Canyon, Santa Catalina Mtns., 26 June 1960, ♀♀ (JAB), 10 July 1962, 4 ♂♂:♀ (ARB), 2 Aug. 1962, ♀ (JAB); Univ. of Arizona, Tucson, 24 July 1962, ♂ (JAB). Yuma Co.: Yuma, 30 June 1957, ♂:5 ♀♀ (VDR).

OXYOPES APOLLO sp. n.

Figures 41, 42, 47-50, 72-75. Map 2.

Oxyopes helius: Bryant, 1936, Psyche, 36(4): 92, fig. 7, ♂, not *O. helius* Chamberlin.

Holotype. Male from Encino, Brooks Co., Texas, 12 May 1952 (M. Cazier, W. Gertsch, R. Schrammel) in the American Museum of Natural History. The specific name is a noun in apposition after the Greek god Apollo.

Discussion. The female holotype of *Oxyopes helius* was described from the Okefenokee Swamp, Georgia, by Chamberlin (1929). Bryant (1936) described what she thought was the male of *O. helius* Chamberlin from Kaufman, Texas, not realizing she had a new species, distinctly different from *O. helius*, a species now placed in the genus *Hamataliwa*.

Structure. Length of 30 females, 4.2 - 6.7 mm. mean 5.2 mm; length of 30 males, 3.4 - 4.4 mm, mean 3.8 mm. Order of leg length IV-I-II-III. For comparison of certain diagnostic measurements of *O. apollo* to those of other species see Table II and Diagram 4.

Color. Female. Pattern illustrated in Figures 41 and 42. Eyes circled in black. Eye region dark brown to black. Face yellow-orange or golden with vertical brown stripes beginning under ALE, widest at AME, narrowing sharply at the lower edge of the clypeus and continuing diagonally to outer margins of chelicerae, midway of basal segment.

Carapace yellow-orange or golden, mostly glabrous. Wide dark brown, irregularly notched and branching submarginal stripes beginning below PLE and continuing to posterior thoracic declivity. Vertical sides yellow-orange, clothed with scattered white hairs.

Dorsum of abdomen with broad median cream to white stripe from base to tip of spinnerets, enclosing a cream colored lanceolate mark over the cardiac region. Brown along margins. Venter with wide brown median longitudinal stripe composed of three indistinct dark bands enclosing two paler ones. Median stripe outlined by white, lateral areas brown.

Legs pale to brownish yellow. Dusky markings heaviest on distal ends of femora, proximal ends of tibiae and ventral surfaces of legs.

Labium brownish yellow to dark brown. Endites brownish yellow with outer margins and distal ends darker gray-brown, except at anterior tip. Sternum cream to yellow with dark brown around margins.

Male. Eye region mostly dark brown or black. Cymbium and leg segments of palpus dark brown. Face yellow-orange or golden with brown stripes originating under ALE, widest at AME, narrowing at clypeus and continuing diagonally to margin of chelicerae midway the length of basal segment. Chelicerae with dark brown distal end.

Carapace glabrous, yellow to golden with submarginal dark brown longitudinal markings similar to those of the female.

Dorsum of abdomen with median longitudinal white stripe enclosing darker lanceolate mark over cardiac region. Lateral areas dark brown or black, sometimes with lighter maculations. Venter of abdomen with brown median stripe from epigastric furrow to base of spinnerets, enclosed by narrow white or yellow stripes. Lateral areas dark brown, usually with pale spots on sides.

Legs yellow to brownish yellow; dusky markings at distal regions of femora, proximal and central portions of tibiae. Markings on femora more pronounced ventrally.

Labium dark brown. Endites dark brown, particularly along margins, with interior color sometimes lighter yellow. Sternum yellow with dark brown perimeter.

Diagnosis. Oxyopes apollo is very similar to *O. floridanus* in structure, color, and in the form of the female genitalia. The chief difference between the two species is in the structure of the patellar apophyses of the males (compare Figs. 74, 75 with Figs. 78, 79). In *O. apollo* the knob of the retrolateral process of the apophysis is much larger than in *O. floridanus.* The specimens of *O. floridanus* have a dense clothing of appressed white hair covering much of the entire body, including the legs, while in *O. apollo* the carapace is often glabrous and there are fewer hairs scattered over the body. If one handles the specimens, the white prostrate hairs are rubbed off, but because a great number of specimens of *O. apollo* were found to have the glabrous carapace, it is probably genuine and not artificially produced. Since the geographic ranges of *O. apollo* and *O.*

floridanus are completely disjunct, based on the material examined, further collections in the interlying area will certainly elucidate their relationship.

In Texas, mature individuals of *O. apollo* seem to be most abundant from May through August. In the southern parts of its range, however, adult males and females of this species have been collected from March through November.

Natural history. Not much is known of the habits or habitat of *O. apollo* despite the large numbers in collections. *Oxyopes apollo* is sympatric over most of its range with *O. salticus,* but, unlike *O. aglossus*, which often appears in collections of *O. salticus, O. apollo* is not taken with *O. salticus.* In Arkansas, *O. apollo* has been captured in pitfall traps, not by sweeping as are *O. salticus* and *O. aglossus.*

Distribution. Tennessee, Missouri, Arkansas south through Oklahoma and Texas, west to Arizona and south through Nuevo Leon and Chihuahua to Hidalgo (Map 2).

Records. Tennessee. Roane Co.: 1 mi. E of Kingston, 12 July 1933, ♀ (WI). *Missouri.* Phelps Co.: Rolla, 9 Sept. 1937, ♀ (RHC). *Arkansas.* Conway Co.: Morrillton, 25 July 1962, 15♂♂:♀ (HEF). Washington Co.: Fayetteville, Aug. 1909, ♀ (R. Thaxter). *Louisiana.* Ascension Par.: Sorrento, 12 Aug. 1938, ♀ (AMD). *Oklahoma.* Harmon Co.: ♀♀. Pawnee Co.: 1.5 mi. W of Cleveland, 16 Aug. 1956, ♀ (MH). *Texas.* Anderson; Brazos; Brewster; Brooks; Hidalgo; Kaufman; Kleberg; Llano; Maverick; Polk; San Patricio; Somervell; Terrell. *New Mexico.* Eddy Co.: 16 mi. S of Artesia, 23 Sept. 1950, ♀ (WJG). *Arizona.* Organ Pipe Cactus Nat. Monument, 3-7 Aug. 1910, ♀.

MEXICO. *Tamaulipas.* San Pedro, May 1936, ♂:8♀♀ (W. A. Green). Santa Teresa, 15 May 1952, 3♀♀:o (MAC, WJG, RS). *Nuevo Leon.* N of Monterey, 8 Aug. 1942, ♂. *Chihuahua.* 50 mi. S of Villa Ahumada, 11 June 1939, ♂♀♀o (AMD, LID). *Hidalgo.* 10 mi. N of Ixmiquilipan, 5 July 1941, ♂ (AMD).

OXYOPES FLORIDANUS sp. n.

Figures 43, 44, 51, 76-79. Map 2.

Holotype. Male from Volusia Co., Florida, 1 Apr. 1939 (H. K. Wallace) in the Museum of Comparative Zoology. The specific name is an adjective referring to the state of Florida.

Structure. Length of eight females, 4.0 - 6.3 mm, mean 4.8 mm; length of two males 3.8 and 4.0 mm. Order of leg length IV-I-II-III. For comparison of certain diagnostic measurements of *O. floridanus* with those of other species see Table II.

Color. Female. Pattern illustrated in Figures 43 and 44. Eyes circled in black with black band from each, directed toward center of eye hexagon. Eye region dark brown, lighter amber in center. Face brownish yellow, pale yellow along lower edge of clypeus. Lighter areas clothed with appressed white hair, especially along sides of face. Vertical brown stripes beginning under ALE, widest at AME, narrowing at cylpeus and continuing diagonally to lateral margins midway down chelicerae.

Carapace light, brownish yellow or golden, with irregular brown pattern as illustrated in Figure 44. Vertical sides light brownish yellow, densely clothed with white hair especially along lower margins.

Dorsum of abdomen with broad median stripe of pale yellow; numerous brown chevrons crossing this stripe posteriorly. Cardiac region with pale brown lanceolate mark. Clothing of ovoid to elliptical flattened hairs forming white patches and giving the abdomen a mottled appearance. Venter of abdomen with wide dark brown stripe from epigastric furrow to base of spinnerets. Median stripe bordered by thin pale brownish yellow to cream stripes. Lateral areas paler than median, brown mottled with brownish yellow to cream. Entire venter overlaid with white hair.

Legs brownish yellow with dusky markings at distal ends of femora and at proximal, central and distal ends of tibiae. Scattered clothing of white flattened hairs heaviest on femora.

Labium brown. Endites brownish yellow with dusky lateral margins; distal ends pale cream. Sternum yellow with dark brown margin, heavily covered with white appressed hair.

Male. Eyes circled in black. Eye region dark brown, almost black. Iridescent scales between AME. Palpi dark brown to black. Face orange-brown with reticulate black markings in one specimen, or entire center of face from ALE to clypeus dark brown in the other case. Dark median area bounded on each side by paler yellow. An indistinct black line from AME to edge of clypeus in one specimen.

Carapace golden brown with wide dark brown longitudinal stripes that have irregular branches and indentations (Fig. 77). Vertical sides golden brown with dense clothing of flattened white hair.

Dorsum of abdomen with central region of pale cream to brownish yellow, covered by dense clothing of translucent scales. Cardiac region outlined with brown. Lateral area brown with scattered patches of white hair posteriorly. Venter with wide brown median stripe, margined by pale lines. Lateral area brown, mottled with white or yellow. Entire venter covered with scattered iridescent scales. Spinnerets pale yellow.

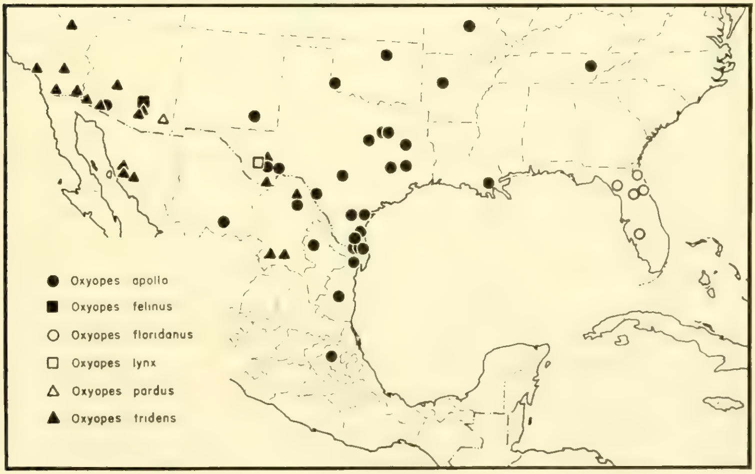
Legs brownish yellow to yellow with scattered dusky markings, more pronounced on ventral surfaces.

Labium dark brown. Endites dark brown with inner margins of distal ends pale. Sternum yellow with dark brown margin.

Diagnosis. Oxyopes floridanus is very similar to *O. apollo.* The primary differences are in the patellar apophyses of the males (compare Figs. 78, 79 with Figs. 74, 75). Since *O. floridanus* is completely allopatric to *O. apollo,* it may be considered only as a geographic race of *O. apollo* when more information becomes available. There are no perceptible differences in the male palpus of *O. apollo* throughout its range from Tennessee to northern Mexico. The male palpus of *O. floridanus,* however, is different from *O. apollo,* and I suspect that this difference would be one of the first brought about by selection pressure during the process of speciation. It appears to me that *O. floridanus* is isolated from *O. apollo,* not only geographically, but genetically as well.

Distribution. Florida (Map 2).

Records. Florida. Desoto Co.: Peace River near Arcadia, 30 Mar. 1938, 6♀♀ (WJG). Duval Co.: 17 Apr. 1949, ♂. Lake Co.: Altoona, ♀♀ (NB). Levy Co.: 2 Mar. 1946, o (HKW). Volusia Co.: 1 Apr. 1939, ♂ (HKW).



Map 2

Oxyopes tridens sp. n.

Figures 45, 46, 53-55, 62, 63, 70, 71. Map 2.

Holotype. Male from Mercury, Nye Co., Nevada, 4 July 1961 (CBA3C) in the American Museum of Natural History. The specific name is an adjective meaning trident.

Structure. Length of 26 females 5.5 - 7.6 mm, mean 6.3 mm; length of 25 males 4.9 - 6.4 mm, mean 5.5 mm. Order of leg length IV-I-II-III. For comparison of certain diagnostic measurements of *O. tridens* with those of other species see Table II and Diagram 4.

Color. Female. Pattern illustrated in Figures 45 and 46. Eye region dark brown with streak of white hairs running from PLE and ALE to PME where it joins white hair of face. Face white from dense clothing of flattened hairs. Wide vertical dark brown stripes originating under ALE, diminishing in size at lower edge of clypeus and continuing to subdistal region of chelicerae. Inner margins and distal ends of chelicerae brown.

Carapace with broad central longitudinal white region, clothed entirely with white hair. Anteriorly this hair forms a trident, the middle prong going between the PME and each of the lateral prongs pointing to a PLE. Broad submarginal stripes of dark brown beginning under ALE and continuing to thoracic declivity. Vertical sides of carapace white.

Dorsum of abdomen with median longitudinal white stripe from base to spinnerets, enclosed on each side by dark brown or black. The dark lateral areas sometimes mottled with white. Venter of abdomen with median brown stripe from epigastric furrow to base of spinnerets, bordered on each side by a thin white line. Lateral area brown, but entire venter often with a clothing of white hairs moderating darker colors.

Legs pale yellow with dusky streaks, especially on ventral surfaces of femora and tibiae. Scattering of white hairs over lower leg surfaces is common. Distal segments are usually somewhat darker.

Endites cream to light brownish yellow with outer margins and sometimes inner margins dusky. Distal ends ivory with black scopulae. Labium pale yellow, grayish along sides with anterior edge ivory.

Male. Pattern illustrated in Figures 62 and 63. Eye region with fewer white hairs than in female. Palpi dark brown or black. The color and markings of the face, carapace, abdomen, legs and other parts of the body are like those of the female and there is very little dimorphism between the sexes.

Diagnosis. Oxyopes tridens is similar in coloration to *O. pardus, O. lynx* and *O. felinus.* Together with these species it forms a distinct species complex related to *O. floridanus* and *O. apollo* in the East. All of the species found in the West appear much the same, with a longitudinal white stripe bordered by black stripes extending the length of the body. *Oxyopes tridens* is the species most often collected in Arizona and the male is easily separated from other species in this group by the patellar apophysis of the palpus (Figs. 70, 71). The female of *O. tridens* is readily identified by the shape of the epigynum (Figs. 53-55), but to date the females of *O. pardus, O. lynx* and *O. felinus* have not been collected and it is not known how much they differ from *O. tridens.*

Natural history. According to W. J. Gertsch (pers. com.) this species is only rarely found on vegetation. It is often seen jumping over rocks in rough outcrops and running over bare ground. This lynx spider has also been collected from the walls of buildings. Of the species I have collected that belong to the *tridens* group, none were found on vegetation. Several were collected in areas where moss was growing and moisture was readily available, but others were collected as they were hopping about over rather dry hillsides. All of my specimens but one are males, however, and these tend to wander more than the females. It is possible that the members of the *tridens* group do not commonly occur on vegetation, as do most other lynxes, but prefer barren hillsides, bare rock outcrops and similar habitats. In many of the vials of *O. tridens* examined during this study only one specimen was present, and only four vials contained more than three specimens. This suggests that *O. tridens* has probably not been collected much by sweeping, since many specimens are found in a single vial where this method is employed. This provides indirect evidence as to the habitat preferences of *O. tridens.*

Distribution. Western Texas to southern Nevada and California, south to Sonora and Coahuila (Map 2).

Records. Texas. Brewster Co.: Marathon, 1-2 July 1916, 3♀♀ (F. E. Lutz); top of Chisos Mtns., Big Bend Nat. Pk., 25-26 July 1933, ♀ (SM). *Arizona.* Maricopa Co.: Phoenix, summer 1959, 6♂♂. Pima Co.: Organ Pipe Cactus Nat. Monument, ♀♀, 14 June 1952, 7oo (MAC, WJG, RS), 3-7 Aug. 1910,

♀♀, 4-7 Aug. 1916, ♀; Sabino Canyon, Santa Catalina Mtns., 1 Sept. 1939, ♀ (RHC), 3 Sept. 1950, ♀ (WJG); Tucson, ♂♂ (O. Bryant), May 1940, o, 20 May 1941, ♀ (RHC), 20 June 1961, ♂, 20 Aug. 1961, ♂ (JAB). Yuma Co.: Yuma, May 1958, ♂, May-June 1956, ♂, 30 June 1957, 3♂♂:4♀♀:o (VDR). *Nevada.* Nye Co.: Mercury, 24 June 1961, ♂, 29 June 1961, ♀, 4 July 1961, ♂, 14 July 1961, ♂, 18 July 1961, ♂, 25 July 1961, ♀. *California.* Imperial Co.: Palo Verde, 14 June 1961, ♂ (VDR). Los Angeles Co.: Acton, 5 Aug. 1931, ♀ (WI). San Bernardino Co.: Twenty-nine Palms, 1-15 July 1945, ♂, July-Aug. 1945, 3♂♂ (J. H. Branch). San Diego Co.: 5 mi. E of Jacumba, 9 July 1960, o(W. F. Barr).

MEXICO. *Coahuila.* La Gloria, 24 Aug. 1947, ♀ (WJG); 20 mi. E of San de las Colonias, 5 July 1936, ♀ (AMD, LID). *Chihuahua.* Samalayuca, 25 June 1947, ♂ (WJG). *Sonora.* El Desemboque, 1-10 Sept. 1953, ♂ (BM); 25 km S of Desemboque, 11 Aug. 1953, ♀ (BM); 10 mi. S of Hermosillo, 16 June 1939, ♀ (AMD, LID).

Oxyopes pardus sp. n.

Figures 60, 61, 68, 69. Map 2.

Holotype. Male from South Fork of Cave Creek Canyon, Chiricahua Mtns., Cochise Co., Arizona, 8 July 1962 (J. A. Beatty) in the Museum of Comparative Zoology. The specific name is a noun in apposition meaning panther.

Structure. Length of two males 4.7 and 5.0 mm. Order of leg length IV-I-II-III. For comparison of certain diagnostic measurements of *O. pardus* with those of other species see Table II.

Color. Male. Pattern illustrated in Figures 60 and 61. Eye region glossy black. Palpi black, thickly clothed with black hair. Iridescent scales between ALE and scattered over clypeus. Face black, with lateral areas paler.

Black color from face continuing posteriorly as two broad submarginal stripes, bounded laterally by yellow. Central area of carapace pale yellow. Vertical sides below black stripes yellow, clothed with white hairs especially along margins of carapace in one specimen.

Dorsum of abdomen with broad median stripe of yellow, clothed with white hair, bordered on each side by black. In one specimen the black is mottled with yellow. In the other, the pale median stripe becomes suffused with gray posteriorly. Venter with broad median dark band from epigastric furrow to spinnerets, bounded on each side by lighter yellow spotted with black in one case. In the other specimen, the venter is entirely black with abundant iridescent scales. This specimen also has iridescent scales on ventral surfaces of femora.

Legs yellow, but with femora appearing gray due to dusky markings. Tibiae and more distal leg segments paler yellow; one specimen has the ventral surface of leg segments dusky.

Endites and labium black with distal ends white. Sternum cream colored with gray around margin.

Diagnosis. Oxyopes pardus is similar in coloration to *O. tridens, O. lynx* and *O. felinus.* All four of these species have the same general coloration (Figs. 56-63). The face of *O. pardus* is much darker than any specimens of the other three species, and it is immediately recognized by the form of the patellar apophysis (Figs. 68, 69). In addition to similar color patterns, the males of the four species above, with the exception of *O. felinus*, each have a well-developed apophysis on the patella, as well as a modification of the tibia.

Natural history. One male of *O. pardus* was collected in the late morning as it was jumping from rock to rock over a rather barren hillside. The other specimen was collected as it ran across an open trail with little ground cover.

Records. Arizona. Cochise Co.: Chiricahua Mtns., South Fork of Cave Creek Canyon, 8 July 1962, ♂ (JAB); Southwestern Research Station, 6 July 1962, ♂ (ARB).

OXYOPES LYNX sp. n.

Figures 58, 59, 66, 67. Map 2.

Holotype. Male from Marathon, Brewster Co., Texas, 12 June 1948 (M. A. Cazier) in the American Museum of Natural History. The specific name is a noun in apposition after the Lynx.

Structure. Length 5.0 mm. Order of leg length IV-I-II-III. For comparison of certain diagnostic measurements of *O. lynx* with those of other species see Table II.

Color. Male. Pattern illustrated in Figures 58 and 59. Eye region black with lighter yellow area in center of hexagon. Face yellow-orange or golden. Vertical stripes of a darker brownish, beginning under ALE and continuing to lower edge of chelicerae, only faintly indicated on chelicerae.

Carapace with median area yellow. Dark brown submarginal stripes from eye region to posterior declivity. Marginal vertical sides clothed with white pubescence.

Dorsum of abdomen with broad white median longitudinal stripe from base to tip of anal tubercle, bordered on each side by black. Black regions with translucent scales. Venter of abdomen dark brown, almost black with translucent, iridescent scales present.

Legs yellow with faint dusky markings on ventral surfaces. Labium and endites yellow. Sternum cream colored with faint dusky markings along margin.

Diagnosis. Oxyopes lynx is related structurally and in general color pattern to the western members of the *tridens* species group, including that species, *O. pardus* and *O. lynx. Oxyopes lynx* is identified by the peculiar shape of the patellar apophysis (Figs. 66, 67) that separates it distinctly from these closely related species.

Chamberlin and Ivie (1944) described a species from the Georgia region of the United States and identified it as *O. lanceolatus* (Walckenaer). Their illustration (Chamberlin and Ivie, 1944, fig. 180) is a retrolateral view (similar to Fig. 66) showing the patellar apophysis. The apophysis of *O. lanceolatus* figured by Chamberlin and Ivie bears a strong resemblance to that of *O. lynx*, and *O. lanceolatus* undoubtedly belongs in the *tridens* species group. Unfortunately, the specimen of *O. lanceolatus* has been misplaced or lost and was not available for examination. An investigation of eastern material did not reveal any specimens resembling its description.

Natural history. Presumably *O. lynx* is similar in ecology to other members of the *tridens* group. Refer to the discussion under the natural history of *O. tridens.*

Records. Texas. Brewster Co.: Marathon, 12 June 1948, ♂ (MAC).

OXYOPES FELINUS sp. n.

Figures 56, 57, 64, 65. Map 2.

Holotype. Male from Molino Basin, Santa Catalina Mtns., Pima Co., Arizona, 12 July 1962 (A. R. Brady) in the Museum of Comparative Zoology. The specific name is an adjective meaning cat-like.

Structure. Length of male 4.6 mm. Order of leg length IV-I-

II-III. For comparison of certain diagnostic measurements of *O. felinus* with those of other species see Table II.

Color. Male. Eye region black, iridescent scales from ALE to AME. Palpi black. Face yellow-orange or golden, with two

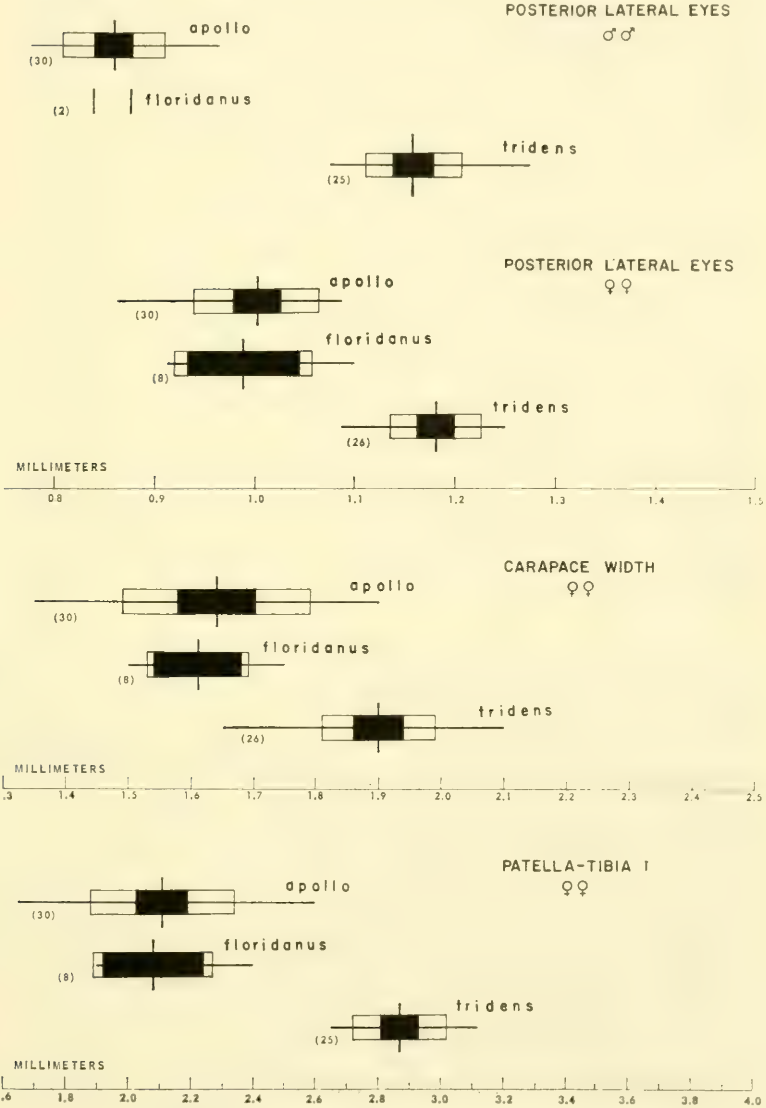


Diagram 4 — Measurements of the *Apollo* Group. For interpretation refer to Diagram 3.

broad vertical black stripes beginning at ALE and continuing to subdistal region of chelicerae. Few scattered scales on face.

Carapace pale yellow. Broad submarginal black stripes from eye region to posterior declivity. Vertical sides of carapace pale yellow.

Dorsum of abdomen with white median longitudinal stripe from base to tip of spinnerets, bordered on each side by jet black. Venter of abdomen black with metallic sheen of lavender or green. Region above epigastric furrow yellow with black patch over the genital region.

Legs yellow with slight dusky markings on ventral surfaces. Legs much lighter than in *O. pardus*.

Labium yellow with black margins, not heavily scopulate. Endites yellow with black scopulae. Sternum pale yellow with dusky marginal markings.

Diagnosis. Oxyopes felinus is similar in coloration to *O. tridens, O. lynx* and *O. pardus*. It does not have a conspicuous patellar apophysis as in the other western species of the *tridens* group, but the color pattern, relative length of the legs and genitalia relate it to this group. *Oxyopes felinus* is most easily recognized by the structure of the male palpus (Figs. 64 and 65).

Natural history. The single male specimen was collected as it ran over very dry vegetation on a rocky slope.

Record. Arizona. Pima Co.: Molino Basin, Santa Catalina Mtns., 12 July 1962, ♂ (ARB).

OXYOPES SALTICUS Hentz

Figures 80-86, 91-96, 104-105. Map 3.

Oxyopes salticus Hentz, 1845, Boston Jour. Nat. Hist., 5:196, pl. 16, fig. 10, ♀. Female syntypes from North Carolina and Alabama, lost. Hentz, 1875, Occ. Pap. Boston Soc. Nat. Hist., 2:47, pl. 6, fig. 10, ♀. Emerton, 1902, Common Spiders of the U. S., Boston, p. 88, figs. 218-219, ♂, ♀. Montgomery, 1902, Proc. Acad. Nat. Sci. Philadelphia, 54: 590, fig. 52, ♀. Comstock, 1912, The Spider Book, p. 660, fig. 773, ♀; *op. cit.*, rev. ed., 1940, p. 668, fig. 733, ♀. Chamberlin, 1929, Ent. News, 40:18, fig. 5, ♀. Kaston, 1948, Bull. Connecticut State Geol. Nat. Hist. Survey, 70, figs. 1147-48, ♀. Roewer, 1954, Katalog der Araneae, 2(a): 333. Bonnet, 1958, Bibliographia Araneorum, 2(4):3240.

Oxyopes astutus Hentz, 1845, Boston Jour. Nat. Hist., 5:197, pl. 17, fig. 1, ♂. Male holotype from Alabama, lost.

Oxyopes gracilis Keyserling, 1877, Verh. Zool.-Bot. Ges. Wien, 26:698, pl. 2, figs. 63, 64, ♀ (in part, but not type).

Discussion. Oxyopes astutus Hentz, is the male of *O. salticus. Oxyopes luteus* Blackwall (1862) and *O. varians* Taczanowski (1873), described from Brazil and French Guiana, respectively, have been erroneously placed in synonymy with *O. salticus* (see Bonnet, 1958, and Roewer, 1954). Keyserling (1877) described *O. gracilis* from the United States, Central and South America. He was dealing with several species. Syntypes are from New Granada (Panama, Ecuador, Peru, Colombia, Venezuela) and this name should be associated with the Central and South American species of *Oxyopes*. The species described as *O. gracilis* Keyserling by F. O. Pickard-Cambridge (1902) is one of the most common *Oxyopes* of Mexico and Central America, and is very similar to *O. salticus*. The male palpus of *O. gracilis* (Figs. 102, 103) is distinct from *O. salticus* (Figs. 104, 105) and so far as I have determined *O. gracilis* occurs from central Mexico southward to Brazil. *Oxyopes salticus* apparently reaches the southern limit of its range in northern Mexico.

Banks (1902, 1903, 1909) reports *O. salticus* from Puerto Rico, Haiti, and Cuba. I have examined very extensive collections from Cuba and smaller ones from Haiti and Puerto Rico and *O. salticus* does not appear in these. Instead, Banks was probably dealing with a closely similar, but very distinct species described from Haiti by Bryant (1948). This species, *O. crewi* Bryant, is abundant in collections from Cuba and evidently replaces *O. salticus* on the islands of Cuba, Haiti and Puerto Rico.

Structure. Length of 30 females 4.6-7.4 mm, mean 5.9 mm; length of 30 males 3.9-5.9 mm, mean 4.7 mm. Order of leg length I-II-IV-III or I-II=IV-III. For comparison of certain diagnostic measurements of *O. salticus* with those of other species see Table II and Diagrams 5 and 6.

Color. Female. Pattern illustrated in Figures 85 and 86. Eye region heavily clothed with white appressed hairs; when rubbed off, the eye region is dark brown to black. Face cream to ivory, white along lower edge of clypeus and distal ends of chelicerae. Black markings along posterior margins or "cheeks" of face as in Figure 85. Vertical black lines from AME to subdistal region of chelicerae.

Carapace pale cream to ivory, with two pairs of dark lines formed by flattened hairs, beginning behind PLE and continuing to thoracic declivity.

Dorsum of abdomen white with cardiac region clothed with white hair and outlined with brown. Two brown stripes posterior to cardiac region formed by appressed hairs. Lateral areas of abdomen dark brown to black with irregular streaks of white hair on the sides. White pigment deposited beneath the integument so that if the clothing of white and contrasting brown hair is rubbed off, the abdomen appears chalk white with the cardiac area translucent white and no darker color laterally. Venter of abdomen with a wide median stripe of brown to black from epigastric furrow to base of spinnerets. Spinnerets pale cream to yellow. Median stripe bounded by white. Lateral areas pale yellow.

Legs pale yellow to cream with longitudinal black stripes on ventral surfaces of femora I, II and III; absent on IV.

Endites pale yellow to cream with distal ends ivory; scopulae black. Labium pale yellow with gray along lateral margins, tip ivory. Sternum pale yellow to cream.

Male. Patterns illustrated in Figures 80-84. Eyes with black band extending from each toward center of eye hexagon. Center of hexagon pale yellow or cream. Eye region glossy; no clothing of white hairs. Iridescent scales between ALE. Face pale yellow to cream. A pair of black marks at margins of face as illustrated in Figure 81. Vertical black lines from AME to subdistal region of chelicerae. Distal ends of chelicerae pale cream. Face between black lines black, and black on chelicerae as indicated in Figure 81, or the vertical lines alone are black as in Figure 83.

Carapace pale yellow to gold with scattering of spatulate appressed hairs sometimes forming faint longitudinal stripes, but never as distinctly as in the female.

Dorsum of abdomen black with covering of iridescent scales giving it a metallic lavender or blue-green luster (Fig. 82). In the field these scales make the abdomen appear golden in bright sunlight. The abdomen ranges from black, as above, to pale yellow tinged with gray (Fig. 84). Cardiac region gray, outlined with pale yellow; scattered glistening scales on the dorsum of lighter individuals. Venter of abdomen black with metallic blue-green or lavender sheen posterior to epigastric furrow. Black patch over genitalic region with areas lateral to this patch yellow. This pattern is found in dark specimens as in Figure 82. The venter may also have a wide median stripe of brown to black, margined with pale lines and the lateral areas pale brownish yellow. This coloration is found in light individuals, as in Figure 84.

Legs pale yellow to cream. Distinct black longitudinal lines on ventral surfaces of femora I, II, III; absent in IV.

Endites yellow to cream with black shading on outer margins or without dusky markings. Labium darker, sometimes brown with distal end pale yellow or cream. Sternum pale yellow or cream, usually with black spots around margin.

Diagnosis. Oxyopes salticus resembles the members of the *acleistus* group in coloration. The black stripes on the femora and the vertical black lines on the face are as in *O. aglossus. Oxyopes salticus* is immediately identified by the peculiar shape of the epigynum (Figs. 91, 93, 96) and the characteristic palpus of the male (Figs. 104, 105). The male palpus has a very stout conical protrusion of the cymbium not as well developed in any other species of *Oxyopes* north of Mexico. Also, a stout brush of short, stiffened bristles (not figured) on the ventral surface of the palpal tibia separates the male of *O. salticus* from all other males.

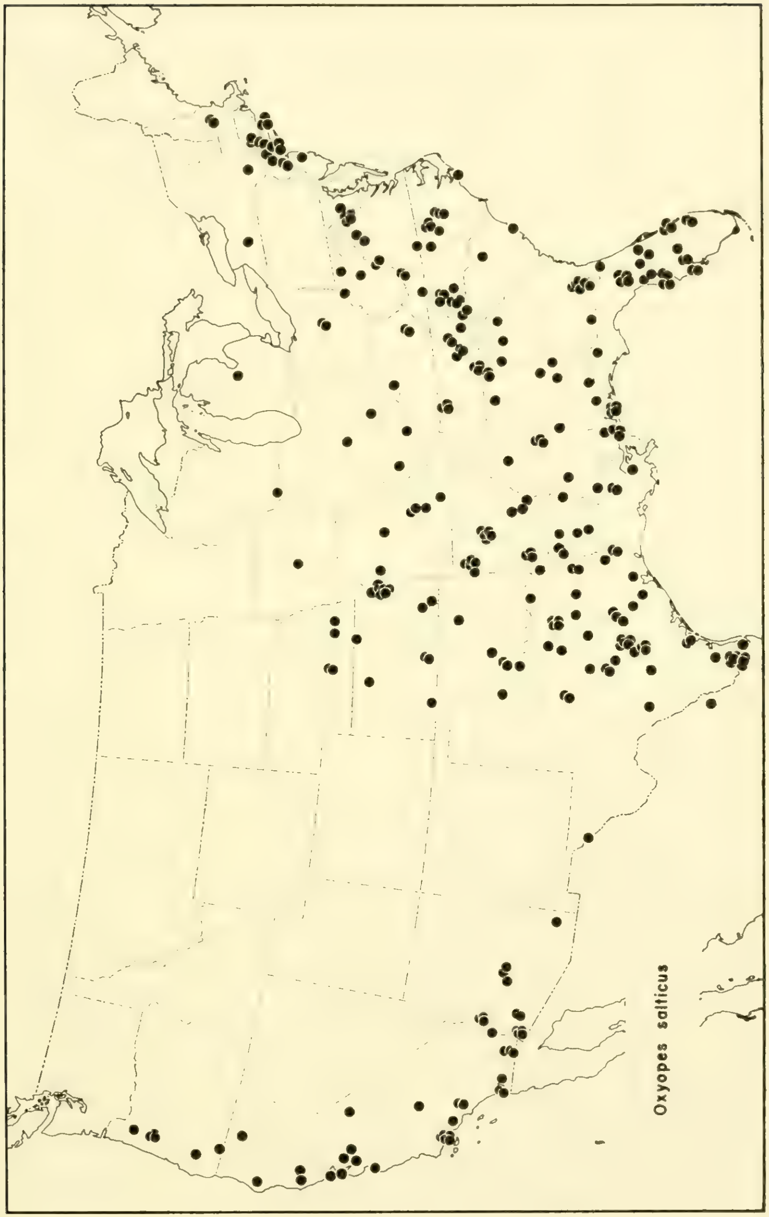
Natural history. Oxyopes salticus is one of the most common spider inhabitants of tall grass and herbaceous vegetation and is found throughout the United States wherever this type of vegetation occurs. During certain seasons, usually mid-June to September, these lynx spiders can be collected in great numbers from vegetation with the aid of a sweep net. The local abundance of these spiders gives evidence of their role as one of the chief predators of insects occurring in grassy or weedy fields and similar habitats. Evidently *O. salticus* is an important predator of certain crop insects, such as those on cotton (Whitcomb, *et al.*, 1963).

As it seeks prey over leafy or grassy vegetation, *O. salticus* assumes a characteristic pose, raising and extending the long front legs and resting on its hind legs. This prey-catching posture is similar to the attitude of some misumenoid crab spiders. Unlike the crab spiders, however, this lynx spider moves about stealthily and pursues its prey more readily, thanks to relatively keen eyesight. If alarmed, *O. salticus* bounds and springs over and through the vegetation with great energy and agility. The leaps of this lynx spider exceed even those of most of the salticids, renowned for their jumping ability. *Oxyopes salticus* is more slender than most Salticidae and its fourth pair of legs is stoutly constructed and well suited for hurling this spider through the air.

Several leaves of grass or similar vegetation are tied together by *O. salticus* or it employs an appropriate small bush or plant to deposit its egg case. Once the egg case is constructed it is fixed among the leaves and twigs with many silken lines forming a tangled meshwork of silk. The female then stands guard over its future progeny much as a mother hen sitting on her nest of eggs. In several hundred vials containing *O. salticus,* only two egg cases were discovered. These were roughly spherical and about 3.5 mm in diameter; one contained 55 spiderlings and the other 18-20 eggs, each a little less than 1 mm in diameter. The extreme rarity of egg cases in collections is probably due to the method used in collecting these spiders. In sweeping, the spiders are dislodged from the vegetation, but the egg cases remain firmly attached.

Distribution. Throughout the United States (Map 3).

Records. County records only are listed. For complete records refer to the Doctoral Dissertation. *New Hampshire.* Hillsboro. *Connecticut.* Fairfield; New Haven. *New York.* Livingston; Nassau; Suffolk; Ulster; Westchester. *New Jersey.* Bergen; Morris; Ocean. *Ohio.* Knox. *District of Columbia. West Virginia.* Marion; Pleasants; Pocahontas; Upshur. *Virginia.* Arlington; Bath; Fairfax; Giles; Page; Pittsylvania; Rockingham. *Kentucky.* Breathitt; Jefferson. *Tennessee.* Hamilton; Knox; Loudon; Roane; Robertson. *North Carolina.* Avery; Buncombe; Burke; Carteret; Durham; Guilford; Haywood; McDowell; Mitchell; Orange; Transylvania; Wake; Yancey. *South Carolina.* Charleston; Kershaw. *Georgia.* Clarke; Dade; Floyd; Fulton; Thomas; Ware. *Florida.* Alachua; Citrus; Desoto; Duval; Highlands; Hillsborough; Indian River; Jackson; Lake; Martin; Orange; Palm Beach; Pasco; Pinellas; Sarasota; Volusia. *Alabama.* Baldwin; Covington; Escambia; Lee; Montgomery; Morgan; Tallapoosa. *Mississippi.* George; Hinds; Jackson; Lafayette; Oktibbeha; Wilkinson. *Louisiana.* Caddo; East Baton Rouge; Grant; Lincoln; Madison; Natchitoches; Orleans. *Michigan.* Midland. *Indiana.* Green; Posey. *Wisconsin.* Lafayette. *Illinois.* Champaign; Washington. *Iowa.* Story. *Missouri.* Boone; Carter; Dent; Jackson; Phelps. *Arkansas.* Conway; Crawford; Deshea; Hempstead; Jefferson; Lincoln; Washington. *Nebraska.* Buffalo; Lancaster; Saline. *Kansas.* Douglas; Greenwood; Jefferson; Kingman; Meade; Montgomery; Rooks; Washington. *Oklahoma.* Comanche; Grady; Harmon; Pawnee. *Texas.* Austin; Bexar; Bowie; Brazos; Burleson; Burnet; Cameron; Cherokee; Dallas; Harris; Hays; Hidalgo; Hudspeth; Jasper; Jim Wells;


Oxyopes salticus

Map 3

Lamar; Liberty; Llano; McLennan; Mills; Navarro; Newton; Panola; San Patricio; Shelby; Somervell; Taylor; Travis; Uvalde; Wichita; Williamson; Wise. *Arizona.* Cochise; Maricopa; Yuma. *Oregon.* Benton; Douglas; Jackson; Yamhill. *California.* Humboldt; Imperial; Kern; Lake; Los Angeles; Marin; Mendocino; Monterey; Riverside; San Diego; San Francisco; San Joaquin; Santa Barbara; Santa Clara; Shasta; Stanislaus; Ventura.

MEXICO. *Nuevo Leon:* 32 mi. SW of Laredo.

OXYOPES SCALARIS Hentz

Figures 87-90, 97-99, 106, 107. Map 4.

Oxyopes scalaris Hentz, 1845, Boston Jour. Nat. Hist., 5:196, pl. 17, fig. 4, ♀. Female syntypes from North Carolina, lost; *ibid.*, 1875, Occ. Pap. Boston Soc. Nat. Hist., 2:47, pl. 7, fig. 4, pl. 19, fig. 120, ♀. Emerton, 1885, Trans. Conn. Acad. Arts Sci., 6:502, pl. 49, fig. 11, ♀, Comstock, 1912, The Spider Book, p. 660; *op. cit.*, rev. ed., 1940, p. 668. Chamberlin, 1929, Ent. News, 40:18, fig. 6, ♀. Kaston, 1948, Bull. Connecticut State Geol. Nat. Hist. Surv., 70:340, pl. 59, fig. 1149, ♀.

Oxyopes laminatus Tullgren, 1901, Bih. Svensk. Vet. Ak. Handl., 27 (4, 1):24, pl. 1, fig. 14, ♀. Female holotype from Orange Co., Florida, in Zoologiska Inst., Uppsala.

Oxyopes cinerea Banks, 1893, Jour. New York Ent. Soc., 1:133. Syntypes from New Hampshire in American Museum of Natural History, examined. NEW SYNONYMY.

Oxyopes rufipes Banks, 1893, Jour. New York Ent. Soc., 1:133. Syntypes (♂:6♀♀) from Olympia, Thurston Co., Washington, in Museum of Comparative Zoology, examined. NEW SYNONYMY.

Oxyopes compacta Banks, 1896, Trans. Amer. Ent. Soc., 23:72. Syntypes (3oo) from Fort Collins, Larimer Co., Colorado, in Museum of Comparative Zoology, examined. NEW SYNONYMY.

Oxyopes pictipes Banks, 1901, Proc. Acad. Nat. Sci. Philadelphia, 53:587. Female holotype from Albuquerque, Bernalillo Co., New Mexico in Museum of Comparative Zoology, examined. NEW SYNONYMY.

Oxyopes classicus Chamberlin, 1925, Proc. Calif. Acad. Sci., 14(4):126, fig. 38, ♀. Female holotype from Altoona, Lake Co., Florida, in Museum of Comparative Zoology, examined. NEW SYNONYMY.

Oxyopes tanneri Chamberlin, 1928, Canad. Ent., 60(4):95. Female holotype from the La Sal Mtns., Utah, in the collection of R. V. Chamberlin, Univ. of Utah, misplaced or lost. NEW SYNONYMY.

Discussion. Oxyopes scalaris is the most widespread of the lynx spiders considered in this investigation. The shape of the epigynum varies somewhat among individuals and the color pattern exhibits a great amount of geographical variation. These two facts have produced an abundance of names in the literature for this species. *Oxyopes laminatus* and *O. classicus* were described from Florida, and *O. tanneri* from Utah. Banks (1893) gave two new names to this species, one to specimens from the state of Washington (*O. rufipes*) and another to specimens from New Hampshire (*O. cinerea*). The separation of these two populations was based on whether the cephalic region of the carapace was elevated above the thoracic region, or on a level with it. If large series are examined, this character varies within the same local populations. The name *O. rufipes* has often been applied to western populations of *O. scalaris,* but only a single species is involved. Chamberlin (1923) used the same criterion as Banks to separate *O. scalaris* from *O. rufipes.* In addition, *O. scalaris* was supposed to have a narrower finger (scape) on the epigynum than *O. rufipes.* The width of the scape also varies in specimens from the same locality as much as it does geographically. Gertsch recognized this synonymy in 1949. Banks (1904) synonymized *O. laminatus* Tullgren with *O. scalaris. Oxyopes tanneri,* judging by its description and locality, is probably *O. scalaris.*

Structure. Length of 30 females 5.8-9.6 mm, mean 6.9 mm; length of 30 males 4.7-6.1 mm, mean 5.5 mm. Order of leg length I-II-IV-III. For comparison of certain diagnostic measurements of *O. scalaris* with those of other species see Table II and Diagrams 5 and 6.

Color. The coloration of *O. scalaris* varies greatly not only geographically, but within the same general areas, e.g. Arizona, California. The color patterns illustrated in Figures 87-90 represent the mode of the California populations. The pattern itself remains similar throughout the range of *O. scalaris* but the shade and intensity of color varies considerably. A detailed color description is given for California specimens of *O. scalaris* and there follows a series of descriptions of the typical variations found in other parts of the United States.

Female. California. Eye region dark brown to black with scattered white hairs. A stripe of white hairs from center of eye hexagon running between ALE and AME and continuing to lower edge of clypeus where it forms a triangular mark. Faint pale white hairs running diagonally outward from each ALE. Face dark brown with lateral areas paler yellowish brown, pale color continuing down chelicerae. Above combination of colors often forming two broad vertical dark brown stripes beginning under ALE, widest at AME, continuing to distal ends of chelicerae. Darker stripes on a background of paler yellowish brown.

Carapace dark brown, almost black with thin line of white hairs from eye region to posterior declivity, joined there by white margin around lower edge of carapace.

Dorsum of abdomen with two basal white stripes that encircle the cardiac region and unite posteriorly where they continue to tip of spinnerets. Posterior to cardiac region this broad stripe is heavily clothed with scale-like hairs and much darker gray-brown. Lateral areas of dorsum dark brown, almost black with two white dashes on each side posteriorly. Anteriorly, the lateral areas may have tufts of white hair intermixed with dark brown or black. White color often expanded in the anterior half of abdomen and visible posteriorly when the spatulate hairs are rubbed off. Cardiac region covered by light brown lanceolate mark, outlined by dark brown or black. Venter of abdomen with wide brown median stripe bounded by white on each side. Lateral areas dark brown or black, mottled with clusters of white hair.

Legs brownish yellow with darker brown on distal halves of femora and on retrolateral surfaces of femora I and II. Brown spots on tibiae as well.

Endites brown with distal ends pale yellow. Labium dark brown. Sternum brown with pale yellow spot in center. Coxae pale yellow or cream.

Arizona. Face and chelicerae very light yellow with darker vertical stripes very faintly indicated. Eye region dark brown with black band from each toward center of eye hexagon.

Carapace light orange with paler yellow center and yellow around margins.

Dorsum of abdomen with paired white bars at base. Most of dorsum yellow with posterior half suffused with orange-brown. Paired spots of yellow posteriorly. Margins of dorsum dark brown. Venter with broad median stripe of brown enclosed by brilliant yellow on each side. Spinnerets light brown.

Legs yellow with few scattered darker markings of brown.

Endites pale yellow or cream. Labium brown. Sternum light brown with large central spot of yellow. Coxae cream.

Colorado. Pattern and color very similar to California populations, but with much of body thickly clothed with appressed white hair giving the spider a much lighter appearance.

Maryland. Eye region dark brown, almost black. Face dark brown with lateral areas paler yellowish brown and a pale yellowish triangular mark mid-way along lower edge of clypeus and two pale spots at lateral edges of clypeus. Chelicerae with vertical dark brown stripes bounded by lighter yellow. Vertical stripes not distinguishable on clypeus.

Carapace dark brown with central longitudinal region somewhat lighter, without paler markings on lower margins of cephalothorax.

Dorsum of abdomen with paired basal white stripes enclosing brown lanceolate mark over cardiac region. Stripes united posteriorly, usually thickly covered by brown hairs giving light brown appearance. Lateral regions dark brown or black. Venter of abdomen with wide median stripe, bordered laterally by slightly narrower white stripes. Sides of abdomen dark brown or black with clusters of white hairs. Very similar to California specimens, but with more black hair giving the spider a gray tinge.

Legs yellowish brown with dusky markings on distal halves of femora; the tibiae with proximal central and distal dark bands.

Male. California. Pattern illustrated in Figures 87 and 88. Eye region dark brown, almost black. Faint line of white hairs from center of eye hexagon, running from ALE to AME. Face dark brown with lighter yellow-brown spots at sides of ALE and along lower edge of clypeus. Chelicerae dark brown with lighter yellowish brown in region of boss and on inner surfaces. Palpi dark brown, almost black.

Carapace dark brown with pale brownish yellow stripe from thoracic groove to posterior edge of carapace. Marginal stripes of brownish yellow.

Dorsum of abdomen with broad central pale stripe from base to spinnerets, forming white margin around brown lanceolate mark of cardiac region. Central stripe covered with dusky scales posteriorly. Thick clothing of translucent scales not producing the iridescent sheen found in *O. salticus,* however. Two white bars on posterior half of abdomen. Lateral regions of dorsum dark brown, almost black. Venter with wide light brown to brown median stripe running length of venter, bordered by stripes of brownish yellow. Lateral regions dark brown with streaks of brownish yellow.

Legs yellowish brown with dusky streaks particularly on femora I and II, streaks not forming any distinct stripe as in *O. salticus.*

Labium brown. Endites yellowish brown with clothing of dusky hair. Sternum brown with pale spot in middle. Coxae cream to yellow.

Arizona. Eye region black with some iridescence. Face dark brown, reticulate with black. Lighter mark on lower edge of clypeus, rather obscure. Palpi dark brown.

Dorsum of abdomen dark brown almost black with dark reddish brown ill-defined spots. Venter with only thin pale lines bordering median stripe.

Legs with dusky bands, particularly on tibiae and metatarsi. Distal half of femora dusky as well.

Michigan. Much lighter in color than California specimens. Face orange-brown with darker reticulations. Eye region dark orange-brown. Palpi dark brown.

Carapace light orange-brown with central area around thoracic groove yellow-orange.

Dorsum of abdomen without definite pattern. A pair of yellow spots is sometimes present on posterior half. Central area of dorsum light orange-brown from thick clothing of dark orange-brown hairs over lighter background. Sides darker brown. Venter with broad median stripe of dark orange-brown bordered by pale yellow area, finely mottled with orange-brown. Sides darker orange-brown.

Legs yellow without dusky markings or only faint traces of darker color.

Labium dark brown. Endites orange-brown with inner tips at distal ends yellow. Sternum dark orange-brown with central elongate yellow spot.

New York. Eye region black. Face gray-brown without black reticulations. Three faint lighter spots along lower edge of clypeus. Palpi brown tinged with gray.

Carapace gray-brown with lighter area posterior to thoracic groove, somewhat lighter around lower margin of carapace.

Dorsum of abdomen with two pale yellow bars near base. Central region mottled cream and brown, tinged with gray. Lateral areas dark brown or black. Two white dashes on each side posteriorly. Venter similar to California specimens.

Legs yellow but appearing darker due to gray pubescence. No definite bands or stripes.

Sternum brown with pale central spot. Coxae cream.

In general the specimens from California, Washington and Oregon are dark brown, almost black, varying to a russet brown with contrasting white or cream markings as in Figures 87-90. In Colorado this species appears somewhat lighter from a heavy clothing of white appressed hair. Populations in Wisconsin and Michigan are much lighter than the western specimens on the average. Along the eastern seaboard the color pattern again becomes very dark and the specimens resemble the darker ones from California, but never have a russet appearance; instead, they have gray overtones produced by black hairs and the face and carapace are very dark gray-brown without lighter markings. In Arizona are found very light colored individuals (see female above) and dark individuals (see male above). The variations in color of the Arizona and West Coast populations may be a result of altitudinal differences. Not enough information is available at present to determine whether this is true. There are no definite clinal changes in color, nor is it possible to correlate color with a particular habitat at this point.

Diagnosis. Oxyopes scalaris is unlike any other North American species of Oxyopidae. The scape of the epigynum is a forwardly directed process as in *O. salticus* (compare Figs. 91-96 with Figs. 97-99), but otherwise these two species bear little resemblance to one another (compare Figs. 80-86 with Figs. 87-90).

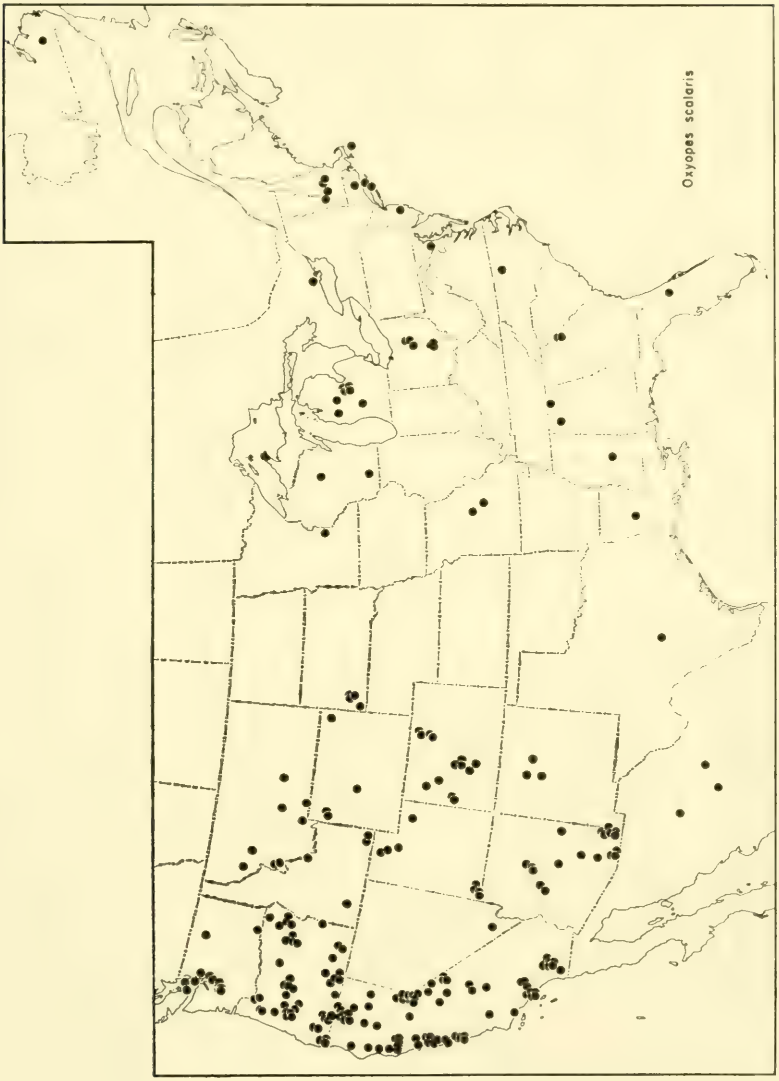
Oxyopes scalaris is most similar to *O. ramosus* of northern Europe and somewhat similar to *O. heterophthalmus* of southern Europe among the species with which I am familiar. Since *O. heterophthalmus* is the type-species of the genus *Oxyopes,* the palpus and epigynum have been figured. The male palpus of *O. heterophthalmus* in retrolateral view (Fig. 101) does not bear any resemblance to that of *O. scalaris,* but the ventral aspect is similar in appearance. The retrolateral view of *O. heterophthalamus* was drawn because the huge tibial apophysis is the trademark, so to speak, of this species. The female epigynum of *O. heterophthalmus* (Fig. 100) is basically similar to that of *O. scalaris,* but the two are obviously distinct species. *Oxyopes scalaris, O. ramosus,* and *O. heterophthalmus* should certainly be considered as belonging to the same species group or subgenus. The distribution of these three species allows one to formulate some interesting zoogeographic theories.

Natural history. Oxyopes scalaris is very common throughout the West on sagebrush (*Artemisia*) and similar shrubs. This lynx spider has been collected in the folowing types of plant associations in California: Pinyon Pine-Juniper Woodland, Montane Forest, Climax Chaparral, Northern Juniper Woodland, Northern Oak Woodland, Juniper Woodland, Coastal Oak Woodland and Sagebrush Scrub. Thus, it does not appear to be restricted to any particular habitat and occurs over a wide range of elevations. In the East, where it is less common, this species has been collected from pine trees, deciduous trees and shrubs, and by sweeping herbaceous vegetation. Habitat-wise *O. scalaris* seems to be widely adaptable; however, in particular parts of its range this lynx spider seems more restricted in its habitat. It is very possible that the habitat preferences change during the life cycle of the spider.

A single egg case collected in Arizona contained 45 embryos. As in the case of *O. salticus,* the egg cases of *O. scalaris* are very seldom collected.

Distribution. From Canada to northern Mexico and from east coast to west coast.

Records. Labrador. 4♀♀ (H. W. Britcher). *British Columbia.* Victoria, 3♀♀ (G. W. Peckham). *Ontario.* Hasting Co.: Frankford, collected 20 Oct. 1961, matured 27 Nov.-5 Dec. 1961, ♂♂:3♀♀ (C. D. Dondale). *Vermont.* Windham. *New Hampshire.* Cheshire; Hillsboro. *Massachusetts.* Nantucket. *Connecticut.* Tolland. *New York.* Suffolk. *New Jersey.* Ocean. *Ohio.* Ashland; Hocking; Wayne. *Maryland.* Prince Georges. *North Carolina.* Durham. *Georgia.* Thompson's Mills, ♂:11♀♀ (NB). *Florida.* Lake Co.: Altoona, ♀. *Alabama.* Lawrence; Madison. *Mississippi.* Scott. *Louisiana.* Grant. *Michigan.* Clare; Ionia; Lake; Midland. *Wisconsin.* Dane; Marathon. *Minnesota.* Hennepin. *Missouri.* Cole; Phelps. *South Dakota.* Custer; Fall River. *Texas.* Llano. *Montana.* Carbon; Gallatin; Meagher; Missoula; Musselshell; Ravalli; Sanders. *Idaho.* Bear Lake; Franklin; Lemhi; Owyhee. *Wyoming.* Crook; Fremont; Teton. *Colorado.* Boulder; Garfield; Gunnison; Larimer; Mesa; Rio Blanco; Saguache. *Utah.* Duchesne; Salt Lake; Washington; Weber. *New Mexico.* Bernalillo; Sandoval; San Miguel. *Arizona.* Apache; Cochise; Coconino; Gila; Graham; Pima; Santa Cruz; Yavapai. *Nevada.* Clark. *Washington.* King; Okanagon; Pierce; San Juan; Snohomish; Thurston; Walla Walla. *Oregon.* Baker; Benton; Clackamas; Crook; Deschutes; Douglas; Grant; Harney; Jackson; Josephine; Klamath; Lake; Lane; Malheur; Multnomah; Union; Wallowa; Wheeler; Yamhill. *California.*


Oxyopes scalaris

Map 4

TABLE II. Measurements of *Oxyopes*

	Species	N	Anterior Lateral Eyes	Posterior Median Eyes	Posterior Lateral Eyes	Carapace Width	Carapace Length
FEMALES	acleistus	7	.648 (.63-.68)	.632 (.61-.66)	1.164 (1.11-1.24)	1.69 (1.6-1.9)	2.29 (2.1-2.5)
	aureus	30	.674±.007(.60-.75)	.662±.007(.60-.75)	1.218±.012(1.10-1.40)	1.84±.03(1.6-2.2)	2.51±.04(2.1-2.9)
	aglossus	30	.599±.004(.56-.64)	.587±.004(.55-.64)	1.078±.008(1.01-1.18)	1.69±.01(1.5-1.8)	2.24±.02(2.0-2.6)
	occidens	10	.789±.015(.72-.88)	.766±.015(.71-.85)	1.418±.029(1.29-1.60)	2.16±.07(1.9-2.5)	2.99±.08(2.6-3.4)
	apollo	30	.540±.007(.46-.59)	.541±.007(.46-.59)	1.002±.012(0.86-1.13)	1.64±.03(1.3-1.9)	2.15±.03(1.7-2.4)
	floridanus	8	.527±.013(.49-.59)	.530±.013(.49-.59)	.989±.024(0.91-1.10)	1.61±.03(1.5-1.8)	2.12±.06(1.9-2.4)
	tridens	26	.659±.006(.60-.71)	.644±.005(.59-.70)	1.181±.009(1.09-1.25)	1.90±.02(1.6-2.1)	2.53±.02(2.2-2.7)
	salticus	30	.539±.006(.49-.60)	.543±.006(.50-.60)	.990±.010(0.89-1.09)	1.78±.03(1.5-2.0)	2.37±.04(2.0-2.8)
	scalaris	30	.626±.007(.55-.71)	.623±.007(.54-.71)	1.121±.013(0.98-1.28)	2.10±.03(1.8-2.6)	2.74±.04(2.3-3.4)
MALES	acleistus	9	.601±.012(.54-.64)	.585±.012(.53-.63)	1.075±.022(0.96-1.15)	1.63±.05(1.4-1.8)	2.13±.04(1.9-2.3)
	aureus	28	.613±.005(.56-.66)	.600±.005(.54-.64)	1.095±.009(1.00-1.21)	1.68±.03(1.4-2.0)	2.21±.02(2.0-2.5)
	aglossus	27	.573±.004(.54-.60)	.558±.004(.51-.59)	1.020±.007(0.95-1.08)	1.66±.02(1.5-1.8)	2.15±.02(1.9-2.3)
	occidens	5	.715 (.68-.75)	.693 (.65-.73)	1.265 (1.20-1.31)	1.99 (1.9-2.1)	2.54 (2.4-2.6)
	apollo	30	.468±.005(.43-.53)	.468±.005(.43-.53)	.858±.009(.78-.96)	1.39±.01(1.3-1.5)	1.81±.03(1.6-2.1)
	floridanus	2	.49 .46	.48 .46	.88 .85	1.3 1.4	1.8 1.9
	tridens	25	.650±.006(.60-.73)	.631±.005(.59-.66)	1.158±.010(1.08-1.28)	1.87±.02(1.6-2.0)	2.41±.02(2.2-2.7)
	pardus	2	.63 .60	.61 .59	1.11 1.05	1.8 1.9	2.2 2.4
	felinus	1	.59	.56	1.01	1.6	2.1
	lynx	1	.58	.55	1.03	1.7	2.3
	salticus	30	.510±.004 (.46-.55)	.510±.005(.46-.56)	.930±.009(0.84-1.00)	1.77±.03(1.4-2.1)	2.25±.04(1.9-2.7)
	scalaris	30	.585±.006(.53-.68)	.574±.006(.51-.66)	1.030±.010(0.95-1.21)	2.04±.03(1.8-2.4)	2.53±.04(2.2-3.1)

TABLE II. Measurements of *Oxyopes* (continued)

	Species	N	Total Length I	Patella-Tibia I	Patella-Tibia II	Patella-Tibia III	Patella-Tibia IV
FEMALES	acleistus	6	8.35 (7.2-8.9)	2.81 (2.4-3.0)	2.62 (2.5-2.8)	1.88 (1.4-2.0)	2.22 (1.8-2.4)
	aureus	30	9.03±.15(7.5-10.6)	3.05±.05(2.5-3.5)	2.77±.05(2.3-3.4)	2.07±.04(1.6-2.4)	2.47±.04(2.0-2.9)
	aglossus	30	8.09±.10(7.2-9.6)	2.74±.04(2.4-3.3)	2.50±.03(2.2-3.0)	1.92±.08(1.6-2.3)	2.21±.03(1.9-2.5)
	occidens	10	10.27±.29(9.8-12.5)	3.70±.10(3.3-4.4)	3.36±.10(3.0-4.0)	2.57±.08(2.3-3.0)	3.04±.08(2.8-3.5)
	apollo	30	6.58±.12(5.2-8.0)	2.11±.04(1.6-2.6)	2.00±.04(1.6-2.4)	1.50±.03(1.2-1.8)	2.26±.05(1.9-2.9)
	floridanus	8	6.60±.21(5.9-7.6)	2.09±.07(1.9-2.4)	2.06±.07(1.7-2.4)	1.46±.05(1.2-1.7)	2.29±.08(2.0-2.7)
	tridens	25	8.87±.09(8.0-10.0)*	2.87±.03(2.6-3.2)	2.63±.03(2.3-2.9)	1.90±.03(1.6-2.2)	2.88±.04(2.5-3.3)
	salticus	30	9.03±.20(6.9-10.9)	3.10±.07(2.4-3.9)	2.85±.07(2.1-3.6)	2.23±.05(1.7-2.8)	2.62±.06(2.0-3.3)
	scalaris	30	9.47±.14(7.8-11.9)	3.25±.05(2.7-3.6)	3.02±.05(2.5-3.9)	2.45±.04(1.9-3.1)	2.68±.04(2.2-3.4)
MALES	acleistus	8	8.81±.20(8.1-9.9)	2.86±.06(2.6-3.2)	2.43±.13(2.4-3.0)	1.83±.04(1.6-2.0)	2.11±.06(1.8-2.4)
	aureus	27	8.89±.14(7.6-10.3)	2.89±.05(2.4-3.4)	2.56±.04(2.1-3.0)**	1.82±.03(1.6-2.1)	2.16±.04(1.8-2.6)
	aglossus	27	8.41±.09(7.6-9.1)★	2.77±.03(2.5-3.0)	2.44±.02(2.1-2.7)★	1.81±.02(1.6-2.0)	2.06±.02(1.8-2.3)
	occidens	5	10.22 (9.9-10.8)	3.32 (3.2-3.5)	2.99 (2.9-3.1)	2.25 (2.1-2.4)	2.59 (2.5-2.8)
	apollo	30	6.37±.07(5.7-7.1)	1.97±.02(1.8-2.2)	1.85±.02(1.6-2.1)	1.36±.02(1.1-1.5)	1.99±.03(1.8-2.4)
	floridanus	2	6.4 6.1	2.0 1.9	1.9 1.8	1.4 1.3	2.0 1.9
	tridens	24	9.51±.09(8.8-10.2)	3.03±.03(2.8-3.3)	2.74±.03(2.5-3.0)	1.96±.03(1.7-2.1)	2.80±.03(2.4-3.0)
	pardus	2	8.3 7.6	2.7 2.5	2.6 2.4	2.0 1.9	2.6 2.4
	felinus	1	7.4	2.4	2.2	1.6	2.3
	lynx	1	8.4	2.7	2.4	1.7	2.6
	salticus	30	8.86±.20(7.1-11.0)	2.85±.06(2.3-3.6)	2.59±.06(2.1-3.3)	2.04±.05(1.6-2.6)	2.34±.05(1.8-3.0)
	scalaris	30	9.99±.16(8.2-12.8)	3.33±.06(2.7-4.4)	3.00±.05(2.4-3.9)	2.36±.04(1.9-3.0)	2.57±.04(2.0-3.3)

*N=24, **N=25, ★N=26. N equals the number of specimens in each sample. All measurements are in millimeters with the *mean* and *standard error* calculated where eight or more specimens were available. The range of the sample is given in parentheses.

Almeda; Alpine; Eldorado; Humboldt; Kern; Lake; Lassen; Los Angeles; Madera; Marin; Mariposa; Mendocino; Mono; Monterey; Napa; Placer; Plumas; Riverside; San Diego; San Francisco; San Luis Obispo; San Mateo; Santa Barbara; Santa Clara; Santa Cruz; Shasta; Sierra; Siskiyou; Tehama; Tulare; Tuolumne.

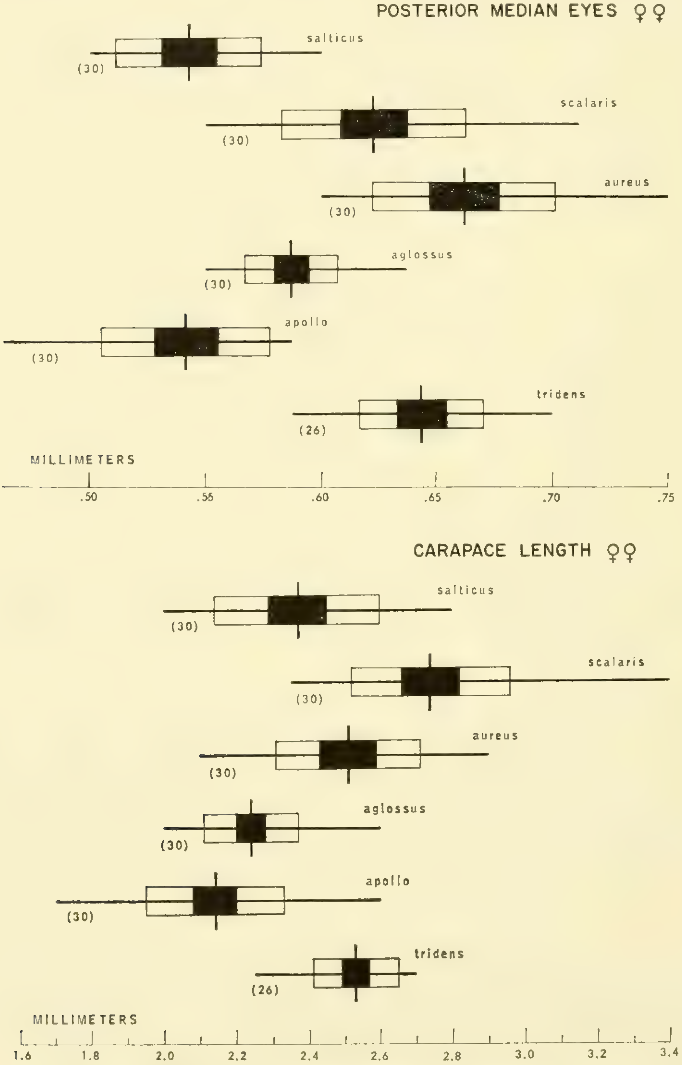


Diagram 5 — Measurements of *Oxyopes*.
For interpretation refer to Diagram 3.

MEXICO. *Chihuahua.* 25 mi. W of Camargo, 13 July 1947, ♂ (WJG); Huejotitlan, 20 July 1947, ♀ (WJG). Matachic, 6 July 1947, ♀ (WJG).

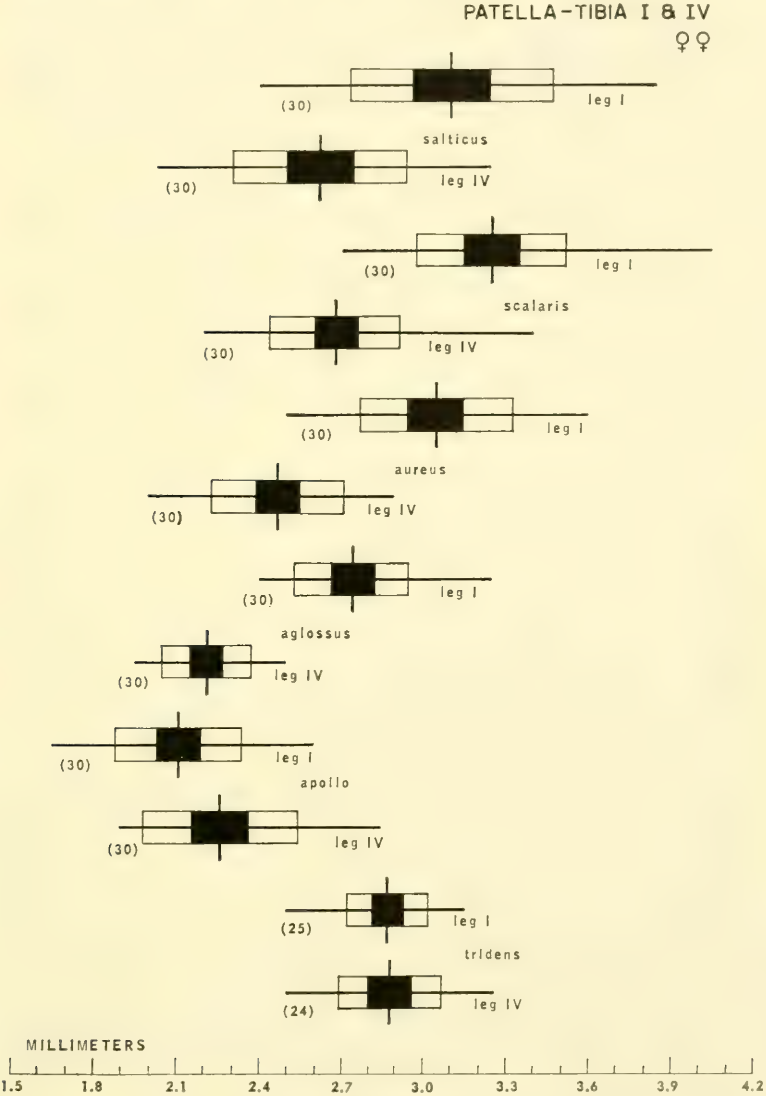


Diagram 6 — Measurements of *Oxyopes*.
For interpretation refer to Diagram 3.

HAMATALIWA Keyserling

Hamataliwa Keyserling, 1887, Verh. Zool.-Bot. Ges. Wien, 6:458, fig. 24, ♀. Type species by monotypy: *Hamataliwa grisea* Keyserling, *op. cit.*, 6:458, fig. 24, ♀, from North America in British Museum (Natural History), examined.

Oxyopeidon O.P.-Cambridge, 1894, Biologia Centrali-Americana, Arachnida, 1:139. Type species designated by F. O. P.-Cambridge, 1902, Biologia Centrali-Americana, Arachnida, 2:346: *Oxyopeidon putum* O. P.-Cambridge, 1894, *op. cit.*, 1:140, in British Museum (Natural History), examined.

Characteristics. Eyes: AME smallest; PME and PLE subequal in size, larger than AME but slightly smaller than ALE. ALE largest.

Width of eye rows variable (Table III). AME row much the smallest, below or in line with the ALE. ALE row wider than PME row (*H. helia*) or PME row much wider than ALE row (*H. grisea, H. unca*). PLE row much the widest. The eyes of *Hamataliwa* generally occupy a much greater comparative space than do the eyes of *Oxyopes* or *Peucetia* (compare Table II with Table III).

Cephalothorax very high and convex, sometimes rectangular in appearance. The vertical slope of the face, however, is much more gradual in *H. grisea* and *H. unca* than in *Oxyopes* or *Peucetia.* Sides of cephalothorax vertical. Carapace often clothed with long hair, and with tufts of hair in eye region.

Labium longer than wide. Endites exceeding the length of labium and converging in front of it.

Abdomen oblong-oval, sometimes quite broad and truncate near the base, more ovate than in *Oxyopes* and *Peucetia.* Long hairs often along sides of abdomen.

Order of leg length I-II-III-IV. The first pair of legs very long and robust. The third pair of legs subequal to or larger than the fourth pair. Fourth pair of legs comparatively weakly developed, unlike *Oxyopes* or *Peucetia.* Legs often with long fringes of hair on the lateral surfaces.

Coloration is cryptic and includes various shades of gray, brown and yellow, with intermixtures of black and white hairs. Together with the rich clothing of long hairs on the legs and body, the color patterns provide excellent concealment against the bark of trees, twigs or woody shrubs. Most species are apparently arboreal.

Female epigyna of similar design throughout the genus, consisting of a shallow median depression enclosed by a circular or horseshoe-shaped, heavily sclerotized posterior rim (Figs. 115-120). Male palpi also similar in basic construction, with the embolus forming a characteristic twisted loop near the base at the mesal edge of the cymbium (Figs. 128-135).

Hamataliwa is easily recognized by the general form of the body, coloration, relative length of the legs, and, above all, by the structure of the genitalia. The arrangement of the eyes is not a valid criterion for separating genera.

HAMATALIWA HELIA (Chamberlin), new combination

Figures 112-114, 119-121, 124, 125, 130-133. Map 5.

Oxyopes helius Chamberlin, 1929, Ent. News, 40:19, fig. 4, ♀. Female holotype from Mixson's Hammock, Okefenokee Swamp, Georgia, in the American Museum of Natural History, examined.

Discussion. Bryant (1936) described what she considered to be the male of *H. helia* (Chamberlin) from Kaufman, Texas. This male is actually a new species, *Oxyopes apollo.*

Structure. Length of 24 females 3.7-5.5 mm, mean 4.6 mm; length of five males 3.2-3.7 mm, mean 3.5 mm. Order of leg length I-II-III-IV. For comparison of *H. helia* with other species see Table III.

Color. Female. Patterns illustrated in Figures 112-114. Eyes outlined with black, with black bands continuing toward center of eye group. Face pale brownish yellow to yellow-orange. Russet spatulate hairs covering much of the clypeus and chelicerae, contributing orange color over yellowish integument. Stripe of white appressed hairs from center of eye hexagon to AME, broader white stripe along sides of face between ALE and PLE to condyle of chelicerae. Tufts of white hair in eye region.

Carapace light brownish yellow to yellow-orange (Fig. 113), sometimes almost white due to dense clothing of flattened white hair (Fig. 114). Sides of carapace darker brown with clothing of dark brown spatulate hairs. Thoracic groove brown.

Dorsum of abdomen pale cream to white with lateral areas darker orange brown (Fig. 113). Sometimes the entire dorsum is white (Fig. 114). Venter of abdomen pale yellow with darker russet color in lateral regions.

Legs yellow to brownish yellow with dusky markings at distal regions of femora and proximal regions of tibiae.

Endites and labium pale yellow, yellow-orange or brownish yellow with distal ends usually lighter. Sternum pale yellow.

Male. Pattern illustrated in Figures 124 and 125. Eyes circled in black with black bands continuing toward center of hexagon. Face brownish yellow to brown with dark gray reticulations, often coalescing to form a gray band at lower edge of clypeus. Tuft of iridescent scale-like hairs between ALE. Cymbium and tibia of palpus dark brown or black. Chelicerae brownish yellow to brown with subdistal white band.

Carapace glabrous, brownish yellow to brown. Darker along sides and to rear of thoracic region where spatulate hairs are present. Scattered iridescent scales on dorsum. Venter of abdomen dark brown or black with central area darkest. Iridescent spatulate scales present. Lung book covers yellow.

Legs pale yellow to brownish yellow with irregular dusky markings and scattered iridescent scales on femora, most conspicuous on prolateral surfaces.

Endites pale yellow to brownish yellow with darker distal border. Labium brownish yellow to brown. Sternum yellow to yellowish brown.

Diagnosis. Hamataliwa helia was described in the genus *Oxyopes* by Chamberlin (1929), probably on the basis of the eye arrangement. The structure of the genitalia, relative length of the legs, general body structure and coloration indicate that *H. helia* properly belongs in the genus *Hamataliwa. Hamataliwa helia* is more like *H. grisea* and *H. unca* than any of the species of *Oxyopes*, especially in the characters noted above. As previously mentioned there are a number of species in Mexico, Central America, the West Indies and in other parts of the world that have been placed in the genus *Oxyopes*, but whose true affinities lie with those lynx spiders comprising the genus *Hamataliwa.*

Hamataliwa helia is much smaller than the other two species of *Hamataliwa* occurring in the United States and is separable on this basis alone. The largest male of *H. helia* is 3.7 mm, the largest female 5.5 mm. The smallest male of *H. grisea* is 4.7 mm, the smallest female 6.2 mm. There are also distinct differences in the eye arrangement of *H. helia* and that of *H. grisea* and *H. unca* (Table III). These three species can also be easily separated on the basis of genitalia, especially in the males (compare Figs. 130-133 with Figs. 128, 129 and Figs. 134, 135).

Natural history. Hamataliwa helia was collected at night from the lower branches of trees at Torreya State Park, Florida, on June 23. At this time most of the females had egg cases. The egg cases were suspended from the tree branches by stout guy-lines and the females, in every case, were tightly gripping the underside of the egg case. In this position, they blend in with the egg cases. The egg cases are somewhat ovoid, but with a definite triangular form and many tiny tufts or teat-like projections. They measure about 5 mm across and examination of two egg sacs disclosed 34 embryos in one and 48 spiderlings in the other. The embryos are about 0.8 mm in diameter.

There were two distinctly different color phases of female in this species, one light brownish yellow or russet (Fig. 113) and the other form completely white above (Fig. 114). A single male was collected at this same locality. As in other species of the genus, *H. helia* seems to be arboreal and is colored to blend in with the twigs or branches of trees. This spider is much more hirsute than any North American species of *Oxyopes*, the hairiness helping to break up the outline of the body against tree bark.

Distribution. Florida to Texas and south to Yucatan (Map 5).

Records. Georgia. Mixson's Hammock, Okefenokee Swamp, 16 June 1912, ♀ (CRC). *Florida.* Alachua Co.: Gainesville, Live Oak Hammock, 23 July 1942, ♀. Liberty Co.: Torreya St. Pk., 22 June 1962, ♀ (JAB), 23 June 1962, ♂ :10♀♀ (ARB, JAB). *Alabama.* Baldwin Co.: Lagoon, 24 Apr. 1951, ♂ (AFA); Bear Foot, 6 June 1957, ♀. Wilkinson Co.: Centerville, Jan.-July 1944, ♀ (AFA). *Texas.* Cameron Co.: Brownsville, ♀ (C. Schaeffer), 8 June 1934, ♀♀ (JNK). Hidalgo Co.: Edinburg, 1934, ♀♀ (SM). Jasper Co.: Jasper, 6 June 1936, ♂ (SM).

MEXICO. *Nayarit.* Jesus Maria, 22-30 June 1955, ♂ oo; La Mesa de Nayarit, 16-21 July 1955, ♀ (BM). *Jalisco.* W side of Lake Sayula, 3 Aug. 1956, ♀ (WJG, VDR). *Oaxaca.* Oaxaca, 4 July 1955, ♀ (CV, PV). *Chiapas.* Ocosingo, 23 June 1950, ♀ (CG, MG). *Yucatan.* Chuminopolis, 15 Aug. 1952, ♂ (JCP, DLP); Uxmal, 16-18 June 1959, ♂ (CV, PV).

HAMATALIWA UNCA sp. n.

Figures 110, 111, 117, 118, 122, 123, 128, 129. Map 5.

Holotype. Male from Edinburg, Hidalgo Co., Texas, Sept.-Dec. 1933 (S. Mulaik) in American Museum of Natural History. The specific name is an arbitrary combination of letters.

Discussion. The male and females considered under this name were not collected together and, therefore, may represent two distinct species. Since the specimens were collected in the same region (southern Texas) and because the sexes agree in eye arrangement, general body form, size and coloration, I have considered them as one species.

Structure. Length of three females 5.9, 6.2 and 7.4 mm; length of male holotype 5.1 mm. Order of leg length I-II-III-IV. For comparison of *H. unca* with other species see Table III.

Color. Female. Pattern illustrated in Figures 110 and 111. Eyes with black bands extending toward center of hexagon; eye region thickly clothed with white hairs, sometimes hiding black bands. Face yellow or yellow-orange to yellowish brown, white hair along lateral regions of face.

Carapace pale brownish yellow overlaid with white hair that is especially abundant along vertical sides. Thoracic groove marked with dark brown.

Dorsum of abdomen cream to pale brownish yellow. In one specimen there is a large spot of thick black hair covering the basal half. When hair is rubbed off, chalk white pigment deposited beneath the integument is disclosed. Venter of abdomen with wide median stripe of gray-brown bordered by cream in one specimen, the median stripe indicated by scattered darker hairs in another, and the third specimen without the median stripe.

Legs yellow with fringes of white hair, most conspicuous on the femora and tibiae. Dark brown annuli at proximal, central and distal regions of metatarsi in one specimen, in another these bands are only faintly indicated, and in the third specimen the metatarsi and tarsi are entirely brown. Palpi fringed with long white hair.

Endites pale yellow to yellow-orange with darker brown along lateral margins. Labium darker brown. Sternum pale yellow to yellow-orange with thick clothing of hair.

Male. Pattern illustrated in Figures 122 and 123. Eyes circled in black with black bands proceeding from eyes toward center of hexagon. Few scattered hairs in eye region, but probably more in the living spider. Face light brownish yellow or amber with scattered darker hairs. Cymbium of palpus brown with distal tip pale.

Carapace glabrous. Pale brownish yellow or amber with sides dark brown or chocolate due to fine points of black pigmentation.

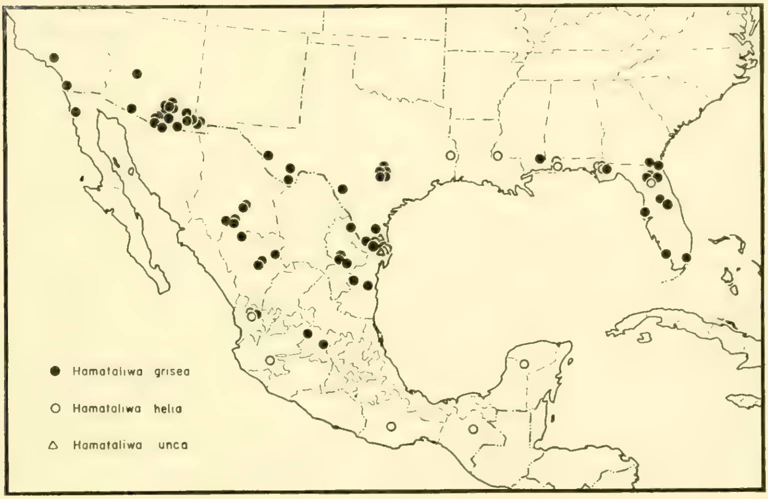
Dorsum of abdomen cream, thickly clothed with white hair. Venter of abdomen darker, pale yellowish brown with no indications of a median stripe.

Legs yellow. Metatarsi with distal, central and proximal dark bands; other segments without darker markings.

Endites yellow. Labium suffused with darker brown. Sternum yellow.

Distribution. Southern Texas (Map 5).

Records. Texas. Cameron Co.: 10 mi. W of Boca Chica, 29 Oct. 1951, ♀ (W. S. Creighton); Brownsville, 8 June 1934, ♀ (JNK); Rangerville, 15 Sept. 1935; ♀ (M. Welch, K. Lamb). Hidalgo Co.: Edinburg, Sept.-Dec. 1933, ♂ (SM).



Map 5

HAMATALIWA GRISEA Keyserling

Figures 108, 109, 115, 116, 126, 127, 134, 135. Map 5.

Hamataliwa grisea Keyserling, 1887, Verh. Zool.-Bot. Ges. Wien, 37:458, pl. 6, fig. 24, ♀. Female holotype from North America, in the British Museum (Natural History), examined.

Hamataliva grisea: Simon, 1898, Histore naturelle des Araignées, 2(2):375, 377, 378, 380, figs. 373, 379. Comstock, The Spider Book, 1912, p. 660; *op. cit.*, rev. ed., 1940, p. 668.

Discussion. Banks (1903), Lutz (1915), and Franganillo (1936) have reported this species from the West Indies. I have not seen any specimens in the large collections available from these islands and assume that these early records are of a similar, but distinct species of which there are several in the West Indies.

Color. Female. Pattern illustrated in Figures 108 and 109. Eyes with black bands extending toward center of eye hexagon. Eye region orange-brown, often thickly clothed with white and black appressed hairs. Face russet, orange-brown or very dark orange-brown, depending on the amount and composition of the hair covering the face. Usually there is a fine clothing of white and black hair intermixed. Lateral regions of face darker brown. Lower edge of clypeus often lighter yellow-orange. Margins of chelicerae dark brown, heavily sclerotized.

Carapace orange-brown to dark orange or reddish brown (mahogany). In the female figured there is a diagonal stripe of white hair on each side from the cheliceral condyle upward to the posterior declivity of the thorax. The posterior declivity of the thorax is usually lighter in color and clothed with white hair. The sides below the diagonal white stripes are dark brown, as they are in the great majority of specimens. In addition, the carapace in most specimens is clothed with fine, intermixed, black and white hair. The black hairs are more abundant along the sides of the carapace, hence the darker color.

Dorsum of abdomen dark brown or black, with small intermingled tufts of black and white hair giving it a dull gray appearance. A few specimens have the abdomen much lighter, pale yellowish brown from a dense clothing of white hair with few or no black hairs. Venter cream to pale yellow or tan without a darker median stripe in nearly all the specimens. A few have a darker median area.

The contrasting dark upper surfaces and the much lighter underside is characteristic of this species.

Legs yellow to brownish yellow, sometimes tinged with orange. Usually long fringes of hair present on the lateral surfaces of the patellae-tibiae. Palpi also with long white hair.

Endites pale brownish yellow with distal ends ivory; scopulae black. Labium pale brownish yellow with sides darker. Sternum soft yellow or pale brownish yellow.

Male. Pattern illustrated in Figures 126 and 127. Eyes with black bands extending toward center of hexagon. Eye region dark brown to almost black. Face russet brown, dark orange-brown to dark brown or black. Sometimes with black reticulations visible against a lighter background. Face clothed with scattered white hairs intermixed with black hair, becoming more abundant laterally. These hairs give a gray overtone. Lower edge of clypeus and ends of chelicerae often lighter yellowish brown. Palpi dark brown or black, with clothing of long black hair and scattered white hairs.

Carapace russet brown, dark orange-brown to dark reddish brown, with clothing of fine black and white hair. Black hair more abundant laterally making sides darker brown or almost black. Thoracic declivity lighter in color, clothed with white, flattened hair. Intermixed fine black and white hairs on carapace often providing a dull gray appearance.

Dorsum of abdomen dark brown overlaid with spots of black and white hair in a salt-and-pepper manner giving it a dull gray appearance. Black hairs sometimes forming irregular bands. Venter of abdomen cream to pale yellowish brown without median stripe.

Legs pale yellowish brown, often with darker orange tinge, and usually lacking the long fringes of hair found in many females. A few specimens have the more distal segments of the legs marked with gray or black bands.

Endites pale yellow or yellowish orange, with ends lighter, ivory. Labium slightly darker with brownish lateral edges. Sternum cream to pale yellow, often suffused with orange.

Diagnosis. Hamataliwa grisea is similar to *H. unca* in size and structure of the body. *Hamataliwa grisea* is usually much darker in color than *H. unca* and slightly larger in size. Table III discloses other differences between these two species. The AME of *H. grisea* form a straight line with the ALE at their lower edges (Figs. 108, 122), but in *H. unca* the AME are below the ALE and form a recurved line from in front (Figs. 110, 122). The male and female genitalia of *H. grisea* (Figs. 115, 116, 134, 135) immediately separate it from *H. unca* and from other Neotropical species of *Hamataliwa*.

Natural history. Although *H. grisea* is occasionally collected by sweeping herbaceous vegetation, it is probably a normal inhabitant of trees and woody shrubs. A male was collected by sweeping Compositae at Goose Island State Park, Aransas Co., Texas. Several females have been taken from guy-lines suspended from trees. One of these females was placed in a glass container and observed. A small twig was placed in the jar with her and she immediately took up a position on the twig with her legs drawn in toward the body and the head downward. In this attitude the spider was perfectly camouflaged against the

TABLE III. Measurements of *Hamataliwa* and *Peucetia*

	Species	N	Anterior Lateral Eyes	Posterior Median Eyes	Posterior Lateral Eyes	Carapace Width	Carapace Length
FEMALES	H. helia	24	.563±.005(.48-.60)	.491±.007(.38-.54)	.961±.010(0.83-1.02)	1.65±.01(1.4-1.8)	2.03±.03(1.6-2.2)
	H. unca	3	1.05 1.12 1.05	1.35 1.44 1.37	1.84 1.95 1.87	2.0 2.4 2.1	2.4 2.7 2.6
	H. grisea	30	1.128±.017(0.95-1.28)	1.504±.022(1.30-1.73)	1.965±.026(1.70-2.23)	2.46±.04(2.0-2.8)	2.87±.04(2.3-3.2)
	P. viridans	30	.992±.015(0.83-1.13)	.698±.011(.60-.80)	1.404±.024(1.18-1.65)	4.57±.10(3.6-5.8)	5.92±.12(4.6-7.5)
	P. longipalpis	30	.989±.014(0.83-1.17)	.688±.009(.60-.80)	1.400±.021(1.18-1.72)	4.66±.10(3.5-6.0)	5.95±.12(4.6-7.9)
MALES	H. helia	5	.467 (.45-.49)	.410 (.38-.44)	.798 (.73-.84)	1.30 (1.2-1.4)	1.67 (1.5-1.8)
	H. unca	1	1.00	1.19	1.69	1.9	2.3
	H. grisea	29	.905±.012(0.77-1.03)	1.186±.018(1.00-1.38)	1.577±.022(1.35-1.77)	2.10±.03(1.7-2.4)	2.45±.04(2.0-2.8)
	P. viridans	30	.792±.011(0.72-0.97)	.565±.009(.48-.69)	1.108±.016(0.95-1.33)	3.72±.08(2.9-4.9)	4.56±.09(3.7-5.8)
	P. longipalpis	30	.794±.013(0.63-0.90)	.571±.010(.45-.65)	1.100±.017(0.83-1.27)	3.73±.07(2.7-4.5)	4.60±.10(3.4-5.4)

			Total Length I	Patella-Tibia I	Patella-Tibia II	Patella-Tibia III	Patella-Tibia IV
FEMALES	H. helia	23	6.46±.10(5.0-7.1)	2.26±.04(1.7-2.5)	2.11±.04(1.6-2.4)	1.62±.03(1.2-1.8)	1.52±.03(1.1-1.7)
	H. unca	3	8.3 9.4 8.7	3.1 3.6 3.4	2.9 3.3 3.0	2.1 2.5 2.3	2.0 2.3 2.2
	H. grisea	30	9.77±.13(8.7-10.9)	3.73±.05(3.0-4.2)	3.40±.05(2.6-3.9)	2.51±.05(1.9-2.9)	2.44±.04(1.9-2.8)
	P. viridans	30	30.96±.65(22.9-38.7)	10.51±.23(7.7-13.0)	9.48±.21(6.7-11.8)	7.52±.18(5.6-9.6)	8.15±.19(5.7-10.0)
	P. longipalpis	30	27.21±.62(20.4-37.0)	9.25±.21(6.8-12.2)	8.46±.20(6.1-11.5)	6.87±.16(5.0-9.2)	7.35±.16(5.6-9.9)
MALES	H. helia	5	5.62 (5.3-5.9)*	1.97 (1.8-2.1)*	1.87 (1.8-2.0)	1.41 (1.3-1.6)	1.26 (1.1-1.4)
	H. unca	1	9.0	3.2	3.0	2.4	2.0
	H. grisea	29	9.70±.14(8.4-11.1)	3.53±.05(3.0-4.0)	3.20±.05(2.6-3.6)	2.36±.04(2.0-2.8)	2.23±.04(1.9-2.6)
	P. viridans	30	33.67±.67(27.1-42.9)	10.45±.21(8.4-13.4)	9.24±.19(7.3-11.9)	6.99±.16(5.2-9.0)	7.63±.17(6.1-9.8)
	P. longipalpis	30	31.20±.73(23.8-40.8)	9.63±.22(7.3-12.4)	8.58±.20(6.3-11.0)	6.66±.16(5.0-8.4)	7.21±.17(5.2-9.0)

*N = 4. N equals the number of specimens in each sample. All measurements are in millimeters with the *mean* and *standard error* calculated where eight or more specimens were available. The range of the sample is bark of the small branch, and she remained in this position even when the twig was removed from the container. This lynx spider remained in a quiescent state and if disturbed used a rapid scuttling motion to escape, much as do some thomisids. Jumping was resorted to only when the spider was greatly disturbed and this act was much less frequent than in spiders of the genus *Oxyopes*.

In Arizona this species was observed on Prickly-Pear Cactus (*Opuntia*), but it is probably more abundant and obviously better hidden on the woody shrubs in this area.

Distribution. Across the southern United States from Florida to California and south to Guanajuato and Jalisco (Map 5).

Records. Georgia. Okefenokee Swamp, June 1912, ♂. *Florida.* Alachua; Collier; Dade; Lake; Liberty; Nassau; Orange; Pinellas; Putnam. *Mississippi.* George. *Texas.* Aransas; Brewster; Cameron; Hidalgo; Jeff Davis; Jim Wells; Starr; Travis; Uvalde. *New Mexico.* Hidalgo. *Arizona.* Cochise; Maricopa; Pima; Santa Cruz. *California.* Los Angeles; San Diego.

MEXICO. Tamaulipas; Nuevo Leon; Chihuahua; Durango; Baja California; Guanajuato; Jalisco.

PEUCETIA Thorell

Pasithea Blackwall 1858, Ann. Mag. Nat. Hist., 3(1):427. Type species by monotypy: *Pasithea viridis* Blackwall, *op. cit.* (3)1:427 from Algeria (Hope Dept. of Entomology, Oxford Univ.). Not *Pasithea* Oken, 1807, a polychaete worm.

Peucetia Thorell, 1869, On European Spiders, Uppsala, 7:196. New name for *Pasithea* Blackwall preoccupied. Thorell, 1869, also designated *Peucetia viridis* (Blackwall) [=*P. littoralis* Simon] as the type of *Peucetia*. *Peucetia viridis* (Blackwall), 1858, is a junior homonym of *Peucetia viridis* (Walckenaer), 1841 [=*P. viridans* (Hentz)].

Characteristics. Eyes: AME smallest; PME and PLE subequal in size, larger than AME. ALE much the largest. Eye rows: AME row much the smallest; ALE row much larger than PME row. PLE row largest. PME and PLE forming only a slightly procurved row, not so procurved as in *Oxyopes*, or *Hamataliwa* (compare Figs. 137, 142 with Figs. 2, 3, 6 and Figs. 109, 111, 114).

Cephalothorax not so high or convex as that of *Oxyopes* or *Hamataliwa*. Carapace narrow in the cephalic region, broadening considerably posteriorly. From above, the carapace of *Peucetia* is much more lycosid in form than that of *Oxyopes* or

Hamataliwa. The face is vertical. Sides of carapace and thoracic declivity not so steep as in *Oxyopes* and *Hamataliwa*, and the eyes of *Peucetia* occupy a comparatively smaller area than in either of these genera.

Labium much longer than wide. Endites very long, slightly enlarged distally and greatly exceeding the length of the labium, converging in front of it.

Abdomen very elongate, almost cylindrical, tapering gradually behind to the spinnerets.

Legs very long in comparison to body length, with many conspicuous black spines. Order of leg length I-II-IV-III.

Integument free of hair except for white hair in eye region. Predominate color of integument is green or shades of green in the living spider. Color is changed rapidly in alcohol.

Male palpus with characteristic paracymbial process in each species, sometimes partly broken off during mating. Palpal sclerites, very similar in the species of *Peucetia* examined (Figs. 154, 155 and 158-161).

Epigyna of females more variable. In all species examined the epigynum is covered or plugged with a hard black matrix, deposited during or immediately after mating.

Peucetia viridis (Blackwall), type-species of the genus, is quite similar to the two species described from the United States.

PEUCETIA VIRIDANS (Hentz)

Figures 136-148. Map 5.

Sphasus viridans Hentz, 1832, Amer. Jour. Sci., 21:105. Syntypes from North Carolina and Alabama, lost.

Clastes abboti Walckenaer, 1838, Hist. Nat. Insectes Aptères, 1:579. Holotype from Georgia, Abbot figure 401.

Clastes viridis Walckenaer, 1841, *ibid.*, 2:475. Holotype from Georgia, Abbot figure 406.

Clastes roseus Walckenaer, 1841, *ibid.*, 2:476. Holotype from Georgia, Abbot figure 411.

Oxyopes viridans: Hentz, 1845, Jour. Boston Soc. Nat. Hist., 5:195, pl. 17, fig. 2, ♀. 1875, Occ. Pap. Boston Soc. Nat. Hist., 2:46, pl. 7, fig. 2, ♀.

Peucetia aurora McCook, 1883, Proc. Acad. Nat. Sci., Philadelphia, p. 277. *Ibid.*, 1890, 2:147, figs. 180, 181. Female holotype from San Bernardino, California, in the Philadelphia Academy of Natural Sciences.

Peucetia viridans: Emerton, 1902, Common Spiders of the United States, p. 89, fig. 220, ♀. Comstock, 1913, The Spider Book, p. 658, figs. 734, 735, ♀; *op. cit.*, rev. ed., 1940, p. 666, figs. 734, 735, ♀. Petrunkevitch, 1929, Trans. Connecticut Acad. Arts Sci., 30:106, figs. 89-91, ♂, ♀. Gertsch, 1949, American Spiders, p. 212, pl. xvii, pl. 31, ♂, ♀.

Peucetia abboti: Chamberlin and Ivie, 1944, Bull. Univ. Utah, (9)35, Biol. Ser. 8(5):134.

Discussion. This species was described under three names applied by Walckenaer (1838, 1841) to the Abbot drawings. The name *Peucetia abboti* was resurrected by Chamberlin and Ivie (1944), but *Peucetia viridans* (Hentz) has priority. *Oxyopes fossanus* Walckenaer, a still earlier name for *P. viridans*, is designated a *nomen oblitum*. The reasons for this are discussed under the section on Walckenaerian names.

Structure. Length of 30 females 11.8-21.6 mm, mean 16.2 mm; length of 30 males 8.3-14.5 mm, mean 11.9 mm. Order of leg length I-II-IV-III. For comparison of diagnostic measurements of *P. viridans* with those of *P. longipalpis*, see Table III.

Color. The vivid green pigment of *Peucetia viridans* washes out rapidly in alcohol, and, therefore, descriptions of the specimens in alcohol are preceded by a short note on these spiders as they appear in nature.

Female. Pattern illustrated in Figures 136 and 137. This pattern is characteristic of well-marked individuals from Arizona and is life-like. Eye region with black bands extending toward center of hexagon. Eye region clothed with white appressed hair. An occasional alcoholic specimen has the eye region red and this is probably the coloration in many living spiders. The face and the entire cephalothorax are a bright, translucent green in life. They are also devoid of hair except in the eye region. The color fades first to a pale green, often with a yellow cast, then becomes pale yellow-orange and sometimes dark yellow-orange. Many parts of the cephalothorax become almost cream in color. Lighter stripes of cream often visible from AME to lower edge of clypeus, which is also often cream colored. Margins of chelicerae usually lighter in color. Sockets of cheliceral condyles at lower margins of clypeus are black.

Specimens from the eastern United States have a pair of bristles one-third the distance from lower edge of clypeus to AME, with distinct black spot at base of each (Fig. 140). A similar pair of bristles with black spots occurs one-third the distance from base to distal ends of chelicerae. In western specimens the bristles are present, but there are no accompanying black spots at the base.

Carapace in alcoholic specimens yellow-orange, tinged with green or faded yellow-green with alternating dark and light bands radiating from thoracic groove. In life the carapace is bright translucent green.

Dorsum of abdomen in living spiders is a bright green with contrasting chalk white markings. The color of the abdomen usually does not fade as rapidly as that of the cephalothorax. In alcoholic specimens the dorsum of abdomen is usually a faded yellow-green or pale green. A translucent, green, cross-shaped mark over the cardiac region, sometimes outlined with white (Fig. 137), is usually present. Often there is a series of four white chevrons beginning at the cardiac region and continuing posteriorly. These chevrons may appear as white spots or bars, and sometimes are reduced to only two pairs near the cardiac region. The median green of the dorsum bordered by white (particularly in specimens from the Southwest), or pale green. Sides pale green with a longitudinal white stripe along ventral edges, often occurring in specimens from the Southwest. Venter with median longitudinal stripe of green, heavily pigmented with white and bordered by white stripes *or* the median longitudinal stripe of chalk-white pigment. Lateral areas pale green to the ventral longitudinal white stripes along sides.

In the living spider the femora are pale green with the more distal segments lighter greenish yellow. Femora with many large black spots (Fig. 138). Black spots at the base of spines on tibiae in specimens from the eastern United States and those from California. Specimens from the Southwest do not usually have these black spots on the tibiae. The legs in living *Peucetia* are often banded with bright red, and there may be red spots over the body as well. Legs in preserved specimens, dark to pale yellow-orange, occasionally tinged with green.

Labium, endites and sternum green in the living lynx spider. In alcoholic specimens the labium is pale yellow-orange, tinged with green. Endites usually cream or pale yellow-orange without green tint. Sternum pale green.

Male. Pattern illustrated in Figures 141 and 142. In life, the male is a vivid translucent green over the entire cephalothorax and abdomen. Eyes with black bands extending toward center of hexagon. Eye region covered with appressed white hair. In museum specimens the variation in color of the cephalothorax and abdomen of the male is very similar to that of the female. The white chevrons or spots on the abdomen are usually not as conspicuous in the male.

The legs, labium, endites and sternum are the same in color as those of the female.

Diagnosis. Peucetia viridans is the most widely distributed oxyopid in this study. It is sympatric over part of its range with *P. longipalpis*, another green lynx spider. These two species are very much alike in color and general appearance as far as I can determine from preserved material. I have not seen *P. longipalpis* in the field. In southern Texas and Arizona, where these two species occur together, *P. longipalpis* has often been mistaken for *P. viridans*. It is also interesting that in a dozen or more vials these two species were mixed, indicating that they occur in close proximity. No differences in ecology have been noted.

The genitalia of *P. viridans* are very distinct from those of *P. longipalpis*, particularly in the males (compare Figs. 158-161 with Figs. 154, 155). In *Peucetia viridans* the legs are much larger in proportion to body size than in *P. longipalpis* (Table III). The male palpus and female epigynum of *P. bibranchiata* (Figs. 149, 150 and 156, 157) are illustrated for comparison with *P. viridans*. From a preliminary study these appear to be separate species, but larger collections, particularly those containing males and females collected together will have to be examined before this is certain. *Peucetia bibranchiata* is found in southern Mexico and Central America.

Natural history. More is known of the natural history of *P. viridans* than of other oxyopids of North America, because of its large size and conspicuous color. Gertsch (1949) reports that many of the western specimens of *P. viridans* inhabit the dull green foliage of wild buckwheat (*Eriogonum fasciculatum*) and that the egg cases are frequently seen near the yellowish flower of this woody shrub. Gertsch (1949) also reports distinctive color variations in *P. viridans*. In Texas I have collected *P. viridans* by sweeping tall grass and weeds in pastures, open fields, and prairie. Egg cases were found in tall grass with the heads of several stems tied together for their attachment. In each instance the female was in close proximity to the egg case.

One female of *P. viridans* was found with its egg case attached to the leaves of an Ash tree (*Fraxinus*). This female and its egg case were collected and observed for several weeks. During this time the female remained in close contact with the egg case. The female guarded the egg sac with great vigor, and when a pencil was poked at the egg case, she left the impressions of her fangs in the soft graphite end. W. H. Whitcomb (1962) has recently reported on egg sac construction and oviposition in *P.*

viridans. A horizontal disk is constructed, and a bowl with an opening on the bottom is built under this disk. The eggs are forced upward into the bowl, the opening closed, and the egg sac completed.

Egg cases of *Peucetia viridans* are encountered more frequently than are the smaller egg sacs of *Oxyopes* or *Hamataliwa.* These egg sacs are rounded, from 1.2-2.5 cm in diameter, flattened on one side and, except in the Southwest, have pointed projections on the surface. The contents of nine egg cases of *P. viridans* with their localities were as follows: three from Florida contained 172 embryos, 189 eggs and 302 embryos; one from Arkansas contained 602 eggs; two from Arizona contained 197 embryos, and 231 eggs; two from Veracruz, Mexico, contained 129, and 158 eggs; and one from Cuba contained 313 spiderlings. *Peucetia,* as expected, produces a great many more eggs than *Oxyopes* or *Hamataliwa.*

The mating behavior of *P. viridans* has not been recorded. The examination of preserved material has revealed several interesting facts. In the great majority of preserved females the epigynum was plugged with a hard, black material, easily removed with a dissecting needle. This material is obviously deposited during or immediately after insemination. Usually imbedded in the material and inserted in the openings of the epigynum are found the two-pronged portion of the paracymbium of the male palpus (Fig. 160). This twin-branched part of the paracymbium of the male palpus is absent in many specimens, indicating that these males have mated. The plugging of the female epigynum and the loss of the paracymbial process of the male apparently occur invariably during mating. These interesting devices appear to prevent further mating by the male, as well as the female. The male with two palpi can, of course, mate twice.

In *P. longipalpis* the paracymbium of the male is not broken off during mating, but the epigynum of the female is closed by a hard plug as in *P. viridans.* The selective advantage of this device that prevents further mating in *P. viridans* is purely conjectural, but it may have been selected for as an isolating mechanism to prevent interbreeding between two closely related sympatric species. It is also possible that the breaking of the male's paracymbium is the by-product of an act of copulation that insures fertilization of the female.

Distribution. Southern United States, Mexico, Central America and the West Indies (Map 6).

Records. Virginia. Nansemond Co.: Holland, 22 July 1945, ♀ o (Buckholz). *Tennessee.* Wilson Co.: Cedars of Lebanon St. Pk., 12 Aug. 1951, ♂ (T. Cohn). *North Carolina.* Carteret; Craven; Duplin; Durham; Orange; Perquimans; Robeson; Wake. *South Carolina.* Bamberg; Charleston. *Georgia.* Baker; Clarke; Lowndes; Rabun; Thomas; Ware; White. *Florida.* Alachua; Bay; Desoto; Escambia; Gadsden; Lake; Marion; Okaloosa; Orange; Pinellas; Polk; Volusia. *Alabama.* Baldwin; Cleburne; Hale; Houston; Lee; Madison; Mobile; Monroe; Montgomery; Tallapoosa. *Mississippi.* Forrest; Madison; Oktibbeha; Warren. *Louisiana.* Ascension; Caddo; East Baton Rouge; Natchitoches; Red River. *Arkansas.* Hempstead; Washington. *Kansas.* Cowley Co.: Winfield, ♂. *Texas.* Aransas; Atascosa; Bexar; Brazos; Cameron; Coryell; Dallas; Hidalgo; Jim Wells; Leon; McLennan; Montgomery; Polk; Sutton; Travis; Walker; Zavala. *Arizona.* Cochise; Pima; Santa Cruz. *California.* Lassen; Los Angeles; Riverside; San Bernardino; San Diego; Santa Barbara.

MEXICO. Tamaulipas; San Luis Potosi; Nuevo Leon; Coahuila; Zacatecas; Chihuahua; Durango; Nayarit; Baja California; Veracruz; Hidalgo; Puebla; Morelos; Guanajuato; Jalisco; Michoacan; Guerrero; Oaxaca; Chiapas; Campeche; Yucatan.

HONDURAS. 27 Km S of Teguigalpa, 12 Oct. 1945, ♀ (A., M. Carr).

NICARAGUA. Santa Maria de Ostuma, Nov. 1959, 3♀♀ (NLHK).

COSTA RICA. Monteverde, Puntarenas, Feb. 1960, ♀, 18 Nov. 1960, ♂ (C. W. Palmer).

PANAMA. Boquete, Chiriqui, Dec. 1946, 4♀♀; Cerro Pena near El Valle, Sept. 1946, ♂ o (NLHK).

CUBA. Habana: Havana, 4♀♀:7oo (F. Cervera); Miramar, 16 Sept. 1951, ♀ (M. Burro); Santiago de las Vegas, ♀ (NB). Las Villas: Soledad, 8 June 1925, ♂ (G. Salt), 3 Aug. 1931, ♂ oo (L. G. Worley), July-Aug. 1932, ♀ o (G. B. Fairchild), 15 Aug. 1930, ♀ (R. P. Dorr). Oriente: Chirivico Harbor, 2-4 July 1955, ♀ (AFA); El Cristo, 3 Oct. 1913, o; Ensenada de Mora, 17 Apr. 1939, ♀ coast below Pico Turquino, 1936, o (PJD). Pinar del Rio: Punta San Juan, 17 July 1947, ♀ (W. L. Nutting); Vinales, 1917, ♀; 7 Km N of Vinales, 16-22

Sept. 1913, ♂ ♀ :4oo; 14 Km N of Vinales, 16-22 Sept. 1913, o.

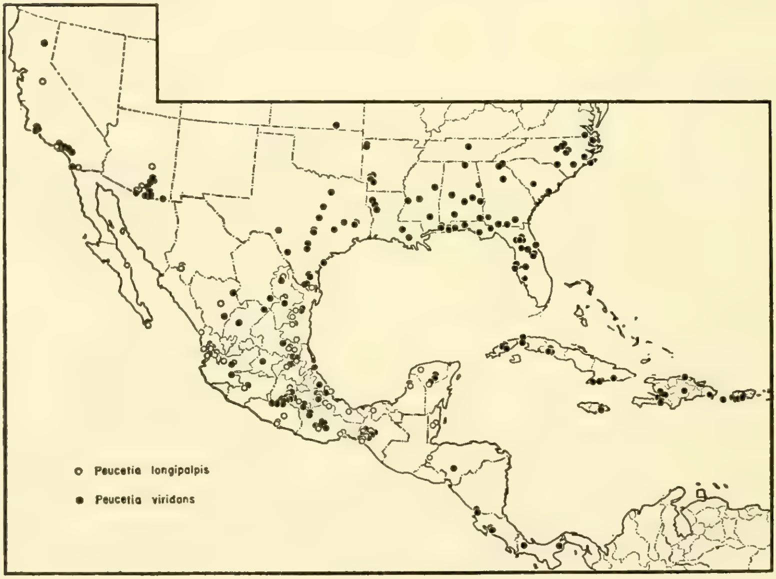
JAMAICA. Hope Botanic Gardens near Kingston, 22 Feb. 1911, ♀ o.

HAITI. Bizeton, 9 Jan. 1922, ♀ ♀ o; Carrefour, 7 Jan. 1922, ♀ (FEW); Furcy, ♀ (W. M. Mann); Kenskoff, ♀ o; Port-au-Prince, ♂, 30-31 Dec. 1921, ♀ (FEW); 25 Km N of Port-au-Prince, 5 Sept. 1934, o (PJD); Trou Caiman, 4 Sept. 1934, o (M. Bates).

DOMINICAN REPUBLIC. Constanza, Aug. 1938, 3oo (PJD); La Romona, 31 July 1935, ♂ (Hassler); Puerto Plata, Apr.-May 1941, 4 ♂ ♂ :4oo (D. Hurst).

PUERTO RICO. Guanica, 3oo; Guayanilla, ♀; Mayaquez, 15-16 Feb. 1914, o; Ponce, ♂ ♀ oo.

MONA ISLAND. Aug. 1944, 3oo (H. Beatty).



Map 6

Peucetia longipalpis F. O. P.-Cambridge

Figures 151-155. Map 5.

Peucetia longipalpis F. O. P.-Cambridge, 1902, Biologia Centrali-Americana, Arachnida, 1:340, pl. 32, fig. 11, ♂. Male holotype from Amula, Guerrero, Mexico, in the British Museum (Natural History), examined.

Discussion. F. O. P.-Cambridge (1902) recognized the male of *P. longipalpis* as a species distinct from *P. bibranchiata* F. O. P.-Cambridge. The female of *P. longipalpis* is figured here for the first time.

Structure. Length of 30 females 12.5-19.6 mm, mean 15.8 mm; length of 30 males 8.1-14.5 mm, mean 11.5 mm. Order of leg length I-II-IV-III. For comparison of certain diagnostic measurements of *P. longipalpis* with those of *P. viridans* see Table II.

Color. There is a good deal of variation in the color of specimens of *P. longipalpis* in alcohol. The following descriptions are based on alcoholic specimens that appear to have retained some of their original pigmentation. In this species, as well as in *P. viridans*, it is difficult to determine the range of color variation in the living animal from preserved specimens because of the alteration produced by the alcohol. The variation in museum specimens is probably greater than that of these spiders in nature.

Female. Eyes with black bands continuing toward center of hexagonal eye area. Eye region clothed with white appressed hair. Face pale orange-yellow with green tinge at lower edge of clypeus and along the margins of chelicerae. Black spots at base of bristles on clypeus and near base of chelicerae as in eastern specimens of *P. viridans*, except that the spots are much smaller in *P. longipalpis*.

Carapace orange-yellow, pale green along sides. The cephalothorax is probably translucent green, like *P. viridans*, in life.

Dorsum of abdomen concolorous, pale green with a thin translucent cross-shaped mark not as conspicuous as that of most specimens of *P. viridans*. White spots and bars on dorsum are apparently absent in *P. longipalpis*. Underlying white pigment shows through the green, especially along the median area; this pigment often makes the abdomen appear white with a green cast. In some specimens the abdomen has presumably faded to a bright yellow. Venter of abdomen with a broad median stripe of chalk-white with greenish tinge. Bordering this stripe is pale green, becoming darker green laterally. No longitudinal white stripes along sides as in many specimens of *P. viridans*.

Legs yellow-orange. Femora with many black spots, but these are usually smaller and less conspicuous than in *P. viridans*. Black spots at base of tibial spines as well.

Labium and sternum pale green. Endites cream, shaded with green.

Male. Coloration very similar to that of the female described above. Palpus yellow-orange with sclerotized portions dark brown.

Most of the males have the abdomen concolorous, pale green to almost white, suffused with green. The cardiac region with only a thin translucent cross-shaped mark. White spots and bars not present on abdomen.

Diagnosis. Peucetia longipalpis is probably very similar in appearance to *P. viridans* in the field. Specimens of *P. longipalpis* are approximately the same size as *P. viridans.* The legs of *P. longipalpis* are, however, much shorter in proportion to body length (Table III). These two species are readily separated by the differences in genitalia (compare Figs. 151-153 with Figs. 143-148), and Figs. 154-155 with Figs. 158-161).

Natural history. Peucetia longipalpis is often collected with *P. viridans* where the ranges of these two species overlap (Map 6), indicating that they occur in similar or adjacent habitats. These two species will probably be readily distinguishable in the field once their habitat preferences or their respective niches are recognized. Nothing is known of the habits or habitat of *P. longipalpis.*

Distribution. Southwestern United States, south to British Honduras (Map 6).

Records. Texas. Cameron Co.: Harlingen, ♀; Harlingen, 8 Oct. 1945, ♂ (D. E. Hardy). *Arizona.* Gila Co.: Parker Creek Wildlife Exp. Stn., 9 Oct. 1959, ♀ (JAB). Pima Co.: Baboquivari Mtns., Brown's Canyon, 9 June 1952, ♂ ♀ ♀ oo (MAC, WJG, RS). *California.* Los Angeles Co.: Los Angeles, ♂ ♀ (NB). San Diego Co.: Lyons Valley, 30 May 1947, ♂ (WMP). Toulume Co.: 5 mi. N of Priest, 8 July 1958, ♂ (WJG, VDR).

MEXICO. Tamaulipas; San Luis Potosi; Nuevo Leon; Coahuila; Chihuahua; Durango; Sinaloa; Nayarit; Baja California; Veracruz; Hidalgo; Puebla; Morelos; Jalisco; Michoacan; Guerrero; Federal District; Oaxaca; Chiapas; Tabasco; Campeche; Yucatan.

BRITISH HONDURAS: El Cayo, Sept. 1959, ♀ ♀ (NLHK); Never Delay, Aug. 1959, ♀ (NLHK).

LIST OF COLLECTORS

AFA	A. F. Archer
AMC	A. M. Chickering
AMD	A. M. Davis
ARB	A. R. Brady
BM	B. Malkin
CG	C. Goodnight
CRC	C. R. Crosby
CSB	C. S. Brimley
CV	C. Vaurie
DCL	D. C. Lowrie
DLP	D. L. Pallister
FEW	F. E. Watson
GN	G. Nelson
HD	H. Dietrich
HEF	H. Exline Frizzell
HKW	H. K. Wallace
HWL	H. W. Levi
JAB	J. A. Beatty
JCP	J. C. Pallister
JHE	J. H. Emerton
JNK	J. N. Knull
LID	L. I. Davis
MAC	M. A. Cazier
MG	M. Goodnight
MH	M. Hite
MN	M. Nirenburg
NB	Nathan Banks
NLHK	N. L. H. Krauss
PJD	P. J. Darlington, Jr.
PV	P. Vaurie
RHC	R. H. Crandall
RS	R. Schrammel
SEJ	S. E. Jones
SM	S. Mulaik
THH	T. H. Hubbell
VDR	V. D. Roth
WI	W. Ivie
WJG	W. J. Gertsch
WMP	W. M. Pearce

This list includes the names of collectors who have collected at two or more localities. Before each name are the initials used to designate that collector in the records of specimens examined. Names of collectors who have collected at only one locality are written in full with the records.

LITERATURE CITED

ABBOT, J. T.

1792. Spiders of Georgia. Manuscript, 116 pp, 116 pls.

BANKS, N.

1893. Notes on spiders. Jour. New York Ent. Soc., **1**:133-134.

1902. Some spiders and other Arachnida from Porto Rico. Proc. U. S. Nat. Hist. (3)**10**:348-360.

1903. A list of Arachnida from Hayti, with descriptions of new species. Proc. Acad. Nat. Sci. Philadelphia, **55**:341.

1904. The Arachnida of Florida. Proc. Acad. Nat. Sci. Philadelphia, **56**:121.

1909. Arachnida of Cuba. Estación central agronómica de Cuba, Second Report, part 2, p. 166.

BLACKWALL, J.

1862. Descriptions of newly discovered spiders captured in Rio Janeiro, by John Gray, Esq., and the Rev. Hamlet Clark. Ann. Mag. Nat. Hist. (3)**10**:348-360.

BONNET, P.

1957-1959. Bibliographia Araneorum. Toulouse, **2**(3):1927-3036; *op. cit.*, 1958, **2**(4):3027-4230; *op. cit.*, 1959, **2**(5):4231-5058.

BOSC, L. A. G.

1800. Araignées de la Caroline. Manuscript, p. 7.

BRADY, A. R.

1962. The spider genus *Sosippus* in North America, Mexico, and Central America (Araneae, Lycosidae). Psyche, **69**(3):129-164.

BRYANT, E. B.

1933. Notes on types of Urquhart's spiders. Rec. Canterbury Mus., **4**:7-8.

1936. New species of southern spiders. Psyche, **36**(4):92-93.

1945. Some new or little known southern spiders. Psyche, **52**(3-4):180-182.

1948. The spiders of Hispaniola. Bull. Mus. Comp. Zool., **100**(4):357-363.

CHAMBERLIN, R. V.

1929. On three new spiders of the genus *Oxyopes*. Ent. News, **40**:17-20.

CHAMBERLIN, R. V. and W. IVIE

1944. Spiders of the Georgia region of North America. Bull. Univ. Utah, biol. ser., **8**(5):1-267.

FORSTER, R.

1955. Spiders from the Subantarctic Islands of New Zealand, Rec. Dominion Mus., **2**(4):186-189.

FRANGANILLO, B. P.

1936. Los Aracnidos de Cuba hasta 1936. La Habana, p. 43.

GERHARDT, U.

1928. Neue biologische Untersuchungen an Spinnen. Zeits. Morph. Ökol. Tiere, **8**(1, 2):105-107.

1933. Neue Untersuchungen zur Sexualbiologie der Spinnen. Zeits. Morph. Ökol. Tiere, **27**(1):28-30.

GERTSCH, W. J.

1949. American Spiders, New York, pp. 94, 212-214.

GLICK, P. A.

1939. The distribution of insects, spiders, and mites in the air. U. S. Dept. Agric. Technical Bull., **673**:19.

HENTZ, N.

1832. On North American spiders. Amer. Jour. Sci. Arts, **21**:106.

KASTON, B. J.

1948. Spiders of Connecticut. State Geol. Nat. Hist. Survey, Connecticut, **70**:783.

KEYSERLING, E. G.

1877. Ueber amerikanische Spinnenarten der Unterordnung Citigradae. Verh. Zool.-Bot. Ges. Wien, **26**:698-700.

LEVI, H. W. and L. R. LEVI

1961. Some comments on Walckenaer's names of American spiders, based on Abbot's drawings. Psyche, **68**(2-3):53-57.

LUTZ, F. E.

1915. List of Greater Antillean spiders with notes on their distribution. Ann. New York Acad. Sci., **26**:103.

McCOOK, H. C.

1888. Necessity for revising the nomenclature of American spiders. Proc. Acad. Nat. Sci. Philadelphia, pp. 74-79.

McCRONE, J. D.

1963. Taxonomic status and evolutionary history of the *Geolycosa pikei* complex in the southeastern United States (Aranea, Lycosidae). Amer. Midl. Nat., **70**(1):47-73.

MARX, G.

1890. Catalogue of the described Araneae of temperate North America. Proc. U. S. Nat. Mus., **12**:567.

PETRUNKEVITCH, A.

1911. A synonymic index-catalogue of spiders of North, Central and South America with all adjacent islands. Bull. Amer. Mus. Nat. Hist., **29**:585.

PICKARD-CAMBRIDGE, F. O.

1902. Biologia Centrali-Americana, Arachnida, Araneidea and Opilones. London, **2**:338-349.

PICKARD-CAMBRIDGE, O.

1894. Biologia Centrali-Americana, Arachnida, Araneidea. London, **1**:139-142.

ROEWER, C. F.

1954. Katalog der Araneae. Bruxelles, **2**(a):315-340.

SIMON, E.

1864. Histoire naturelle des Araignées (Aranéides). Paris, p. 387.

1898. Histoire naturelle des Araignées. Paris, **2**:370-380.

SUZUKI, S.

1952. Cytological studies in spiders, II. Jour. Sci. Hiroshima Univ., Hiroshima, ser. B, div. 1, **13**:44-47.

TACZANOWSKI, L.

1873. Les Araneids de la Guyane française. Horae Soc. Ent. Ross., **9**:95.

THORELL, T.

1869. On European spiders. Uppsala, p. 197.

WALCKENAER, C. A.

1805. Tableau des Aranéides ou caractères essentiels des tribus, genres, familles et races que renferme le genre *Aranea* de Linné, avec la désignation des espèces comprises dans chacune de ces divisions. Paris, p. 20.

1838-1841. Histoire naturelle des insectes Aptères. Paris, **1**:1-682; *op. cit.*, 1841, **2**:1-549.

WALLACE, H. K.

1942a. A revision of the burrowing spiders of the genus *Geolycosa* (Araneae, Lycosidae). Amer. Midl. Nat., **27**(1):1-62.

1942b. A study of the *lenta* group of the genus *Lycosa*, with descriptions of new species (Araneae, Lycosidae). Amer. Mus. Nov., no. 1185:1-21.

WHITCOMB, W. H.

1962. Egg sac construction and oviposition of the green lynx spider, *Peucetia viridans* (Oxyopidae). Southwestern Nat., **7**(3-4):198-201.

WHITCOMB, W. H. *et al.*

1963. Spiders of the Arkansas cotton field. Ann. Ent. Soc. America, **56**:653-660.

PLATES

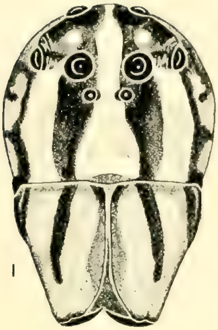
PLATE I

FIGS. 1-4. *Oxyopes aureus* sp. n. 1-2. Female holotype from Bentsen St. Pk., Hidalgo Co., Texas, 30 June 1962. 1. Face view. 2. Dorsal view. 3-4. Female paratype from Bentsen St. Pk., Hidalgo Co., Texas, 30 June 1962. 3. Dorsal view. 4. Left leg I, prolateral view.

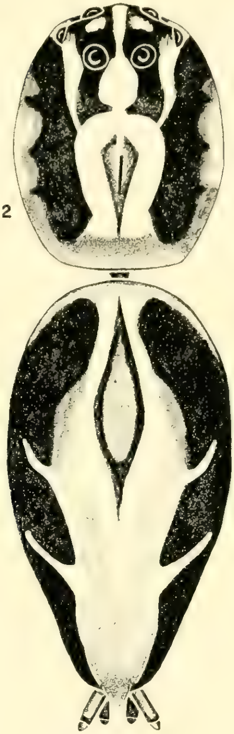
FIGS. 5-6. *Oxyopes acleistus* Chamberlin, female from Gold Head Branch St. Pk., Putnam Co., Florida, 13 June 1962. 5. Face view. 6. Dorsal view.

Scale is for dorsal view and leg only. The face view is slightly larger.

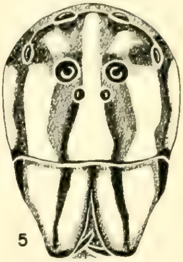
1



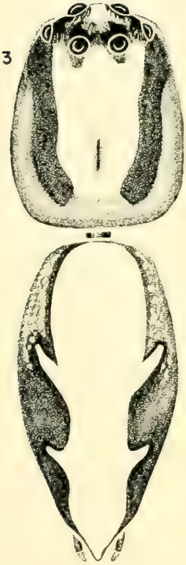
2



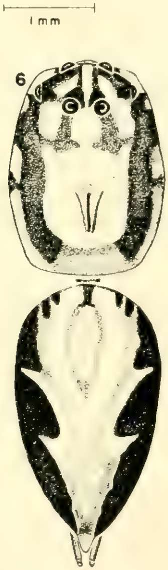
5



3



6



4

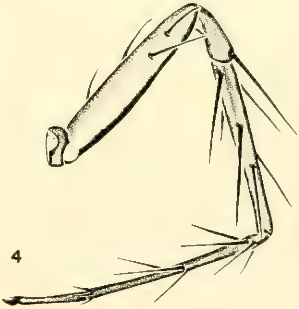
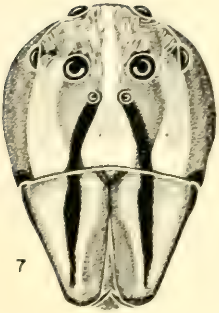


PLATE II

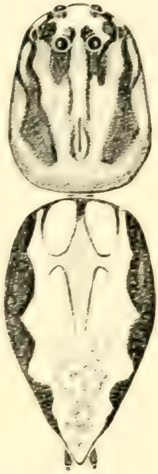
Figs. 7-8. *Oxyopes occidens* sp. n., female from Sabino Pond, Sabino Canyon, Santa Catalina Mtns., Pima Co., Arizona, 10 July 1962. 7. Face view. 8. Dorsal view.

Figs. 9-12. *Oxyopes aglossus* Chamberlin. 9-11. Female from Duke Forest, Durham, Durham Co., North Carolina, 13-18 June 1933. 9. Dorsal view. 10. Labium, endites and sternum, ventral view. 11. Face view. 12. Dorsal view of female from Woodworth, Rapides Par., Louisiana, 21 June 1941.

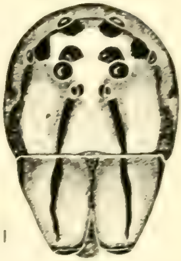
Scale is for dorsal view only. The face view is slightly larger. Labium, endites and sternum are three times larger than scale for dorsal view.



7

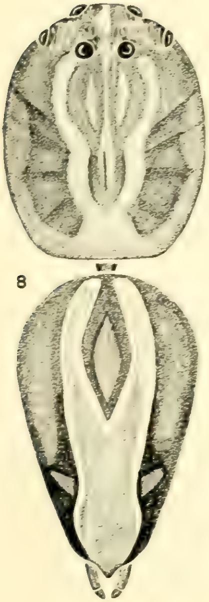


9

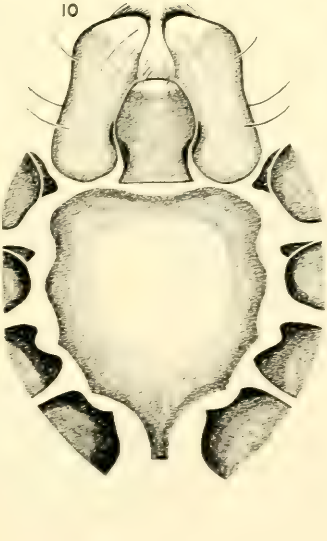


11

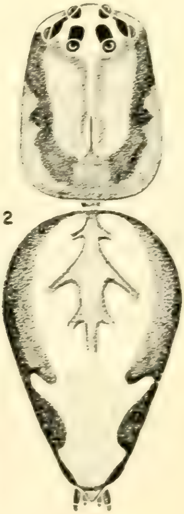
1 mm



8



10



12

PLATE III

Figs. 13-17. *Oxyopes aureus* sp. n. 13-14. Female paratype from Bentsen St. Pk., Hidalgo Co., Texas, 30 June 1962. 13. Internal genitalia, dorsal view. 14. Epigynum. 15-16. Female holotype from Bentsen St. Pk., Hidalgo Co., Texas, 30 June 1962. 15. Internal genitalia, dorsal view. 16. Epigynum. 17. Epigynum of female paratype from Bentsen St. Pk., Hidalgo Co., Texas, 30 June 1962.

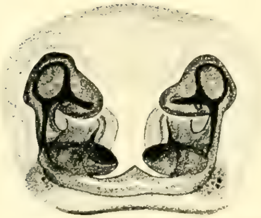
Figs. 18-20. *Oxyopes aclcistus* Chamberlin. 18-19. Female from Florida, Highlands Hammock St. Pk., Highlands Co., Florida, 21 June 1962. 18. Internal genitalia, dorsal view. 19. Epigynum. 20. Epigynum of female from Gold Head Branch St. Pk., Putnam Co., Florida, 13 June 1962.

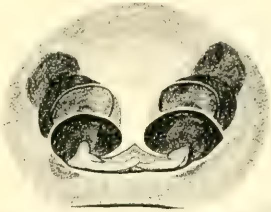
Figs. 21-22. *Oxyopes aglossus* Chamberlin, female from Duke Forest, Durham, Durham Co., North Carolina, 13-18 June 1933. 21. Female genitalia, dorsal view. 22. Epigynum.

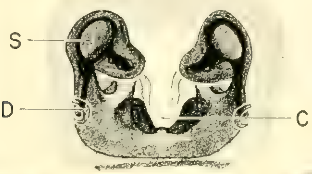
Figs. 23-24. *Oxyopes occidens* sp. n., female from Sabino Pond, Sabino Canyon, Santa Catalina Mtns., Pima Co., Arizona, 10 July 1962. 23. Internal genitalia, dorsal view. 24. Epigynum.

Abbreviations. C, central cavity; D, fertilization duct; R, anterior sclerotized rim; S, seminal receptacle.

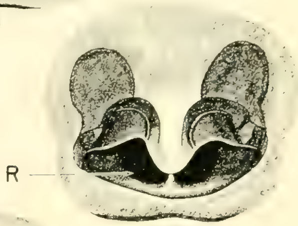
Scale is the same for the epigyna of *all* species, except *Peucetia.*


13

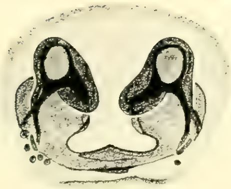

14

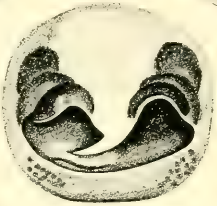


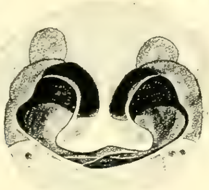
15

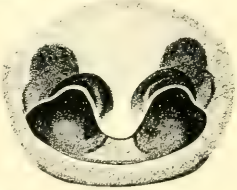


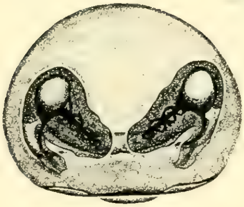
16

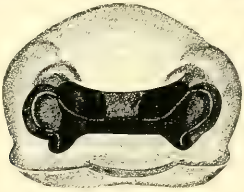

18

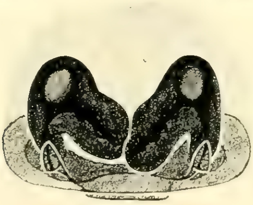

17

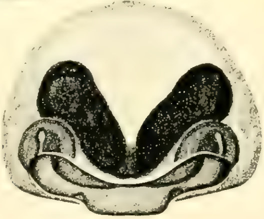

19


20


21


22


23


24

0.1 mm

PLATE IV

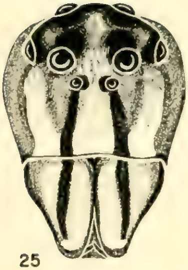
Figs. 25-26. *Oxyopes occidens* sp. n., male holotype from Sabino Pond, Sabino Canyon, Santa Catalina Mtns., Pima Co., Arizona, 10 July 1962. 25. Face view. 26. Dorsal view.

Figs. 27-28. *Oxyopes aureus* sp. n., male from Bentsen St. Pk., 21 June 1962. 27. Face view. 28. Dorsal view.

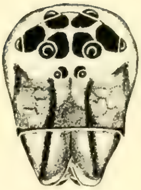
Figs. 29-30. *Oxyopes acleistus* Chamberlin, male from Highlands Hammock St. Pk., 21 June 1962. 29. Face view. 30. Dorsal view.

Figs. 31-32. *Oxyopes aglossus* Chamberlin, male from Duke Forest, Durham, Durham Co., North Carolina, 13-18 June 1933. 31. Face view. 32. Dorsal view.

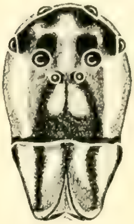
Scale is for dorsal view only. The face view is slightly larger.



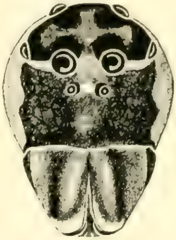
25



31

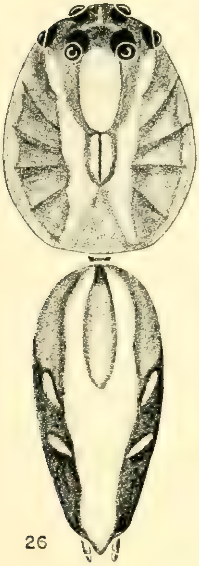


29

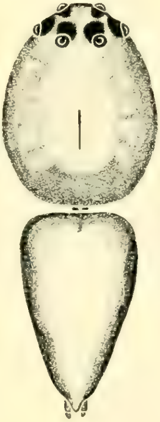


27

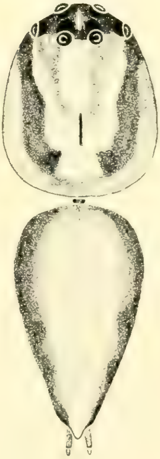
1 mm



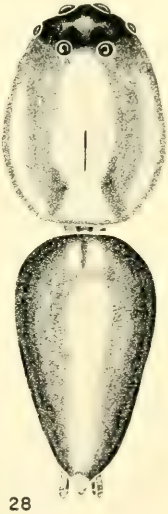
26



32



30



28

PLATE V

FIGS. 33-34. *Oxyopes occidens* sp. n., male holotype from Sabino Pond, Sabino Canyon, Santa Catalina Mtns., 10 July 1962. 33. Left palpus, retrolateral view. 34. Left palpus, ventral view.

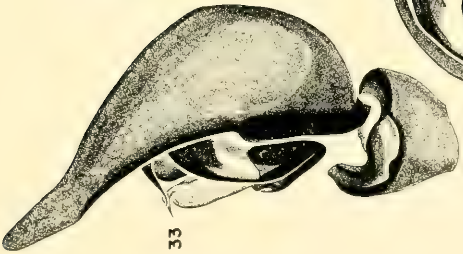
FIGS. 35-36. *Oxyopes aureus* sp. n., male from Bentsen St. Pk., Hidalgo Co., Texas, 30 June 1962. 35. Palpus, retrolateral view. 36. Palpus, ventral view.

FIGS. 37-38. *Oxyopes acleistus* Chamberlin, male from Highlands Hammock St. Pk., Highlands Co., Florida. 37. Palpus, retrolateral view. 38. Palpus, ventral view.

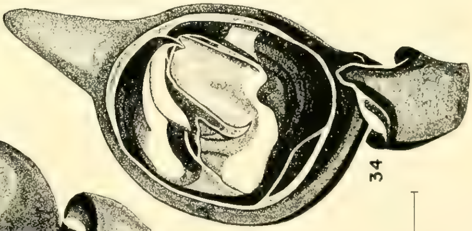
FIGS. 39-40. *Oxyopes aglossus* Chamberlin, male from Duke Forest, Durham, Durham Co., North Carolina, 13-18 June 1933. 39. Palpus, retrolateral view. 40. Palpus, ventral view.

Abbreviations. C, conductor of embolus; E, embolus; L, lamellar apophysis; T, tibial apophysis.

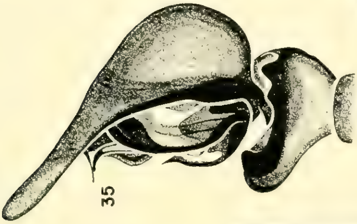
The scale is the same for the palpi of *all* species, except *Peucetia*.



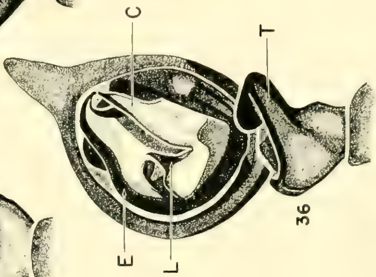
33



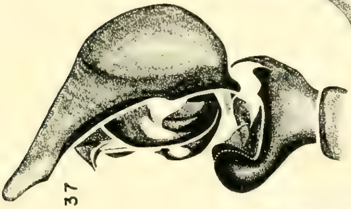
34



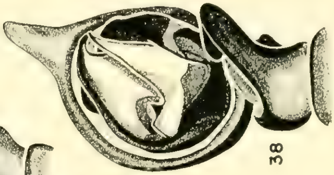
35



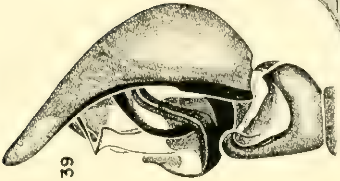
36



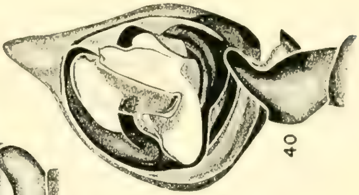
37



38



39



40

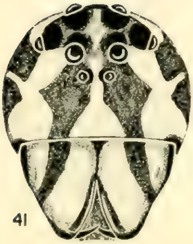
PLATE VI

FIGS. 41-42. *Oxyopes apollo* sp. n., female from Glen Rose, Somervell Co., Texas, 15 June 1940. 41. Face view. 42. Dorsal view.

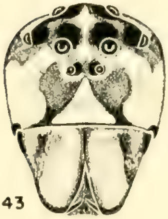
FIGS. 43-44. *Oxyopes floridanus* sp. n., Peace River near Arcadia, Desoto Co., Florida, 30 Mar. 1938. 43. Face view. 44. Dorsal view.

FIGS. 45-46. *Oxyopes tridens* sp. n., female from Mercury, Nye Co., Nevada, 29 June 1961. 45. Face view. 46. Dorsal view.

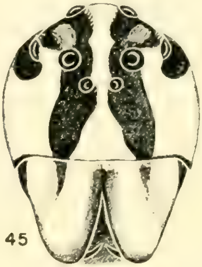
Scale is for dorsal view only. The face view is enlarged slightly more.



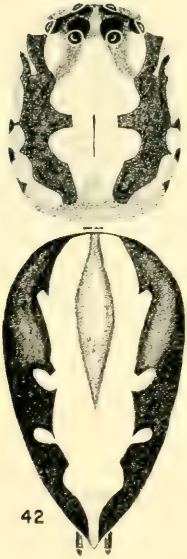
41



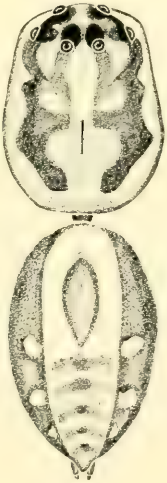
43



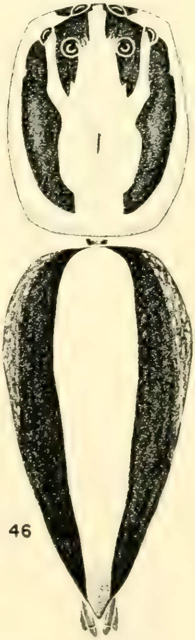
45



42



44



46

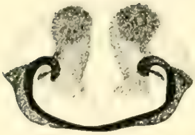
1 mm

PLATE VII

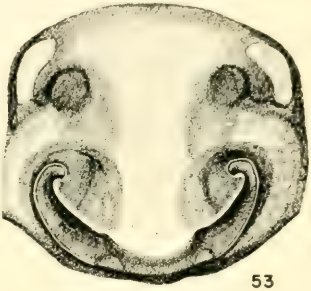
FIGS. 47-50. *Oxyopes apollo* sp. n., female from Marathon, Brewster Co., Texas, 12 June 1948. 47. Epigynum. 48. Internal genitalia, dorsal view. 49. Left leg I, prolateral view. 50. Left leg IV, prolateral view.

FIGS. 51-52. *Oxyopes floridanus* sp. n., female from Peace River near Arcadia, Desoto Co., Florida, 30 Mar. 1938. 51. Epigynum. 52. Internal genitalia, dorsal view.

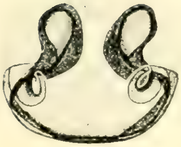
FIGS. 53-55. *Oxyopes tridens* sp. n. 53. Epigynum of female from Mercury, Nye Co., Nevada, 29 June 1961. 54-55. Female from Mercury, Nye Co., Nevada, 25 July 1961. 54. Epigynum. 55. Internal genitalia, dorsal view.



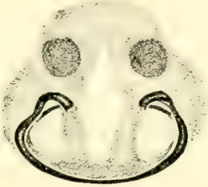
47



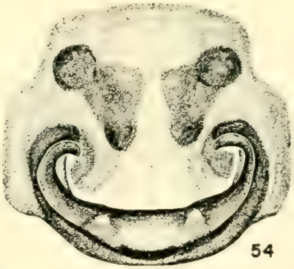
53



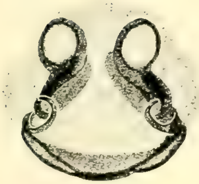
48



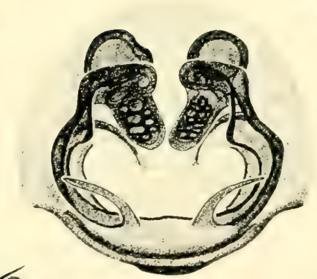
51



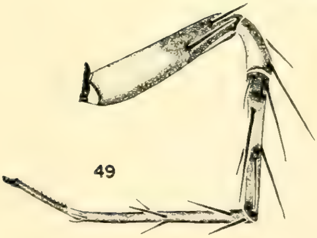
54



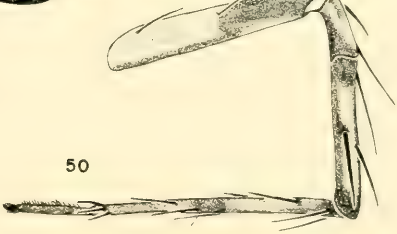
52



55



49



50

PLATE VIII

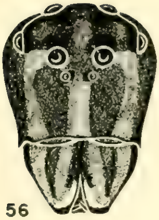
Figs. 56-57. *Oxyopes felinus* sp. n., male holotype from Molino Basin, Santa Catalina Mtns., Pima Co., Arizona, 12 July 1962. 56. Face view. 57. Dorsal view.

Figs. 58-59. *Oxyopes lynx* sp. n., male holotype from Marathon, Brewster Co., Texas, 12 June 1948. 58. Face view. 59. Dorsal view.

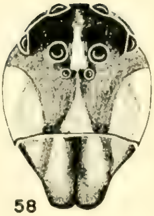
Figs. 60-61. *Oxyopes pardus* sp. n., male holotype from South Fork of Cave Creek Canyon, Chiricahua Mtns., Cochise Co., Arizona, 8 July 1962. 60. Face view. 61. Dorsal view.

Figs. 62-63. *Oxyopes tridens* sp. n., male holotype from Mercury, Nye Co., 4 July 1961. 62. Face view. 63. Dorsal view.

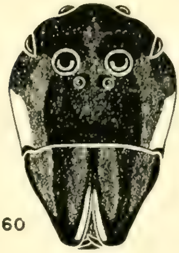
Scale is for dorsal view only. The face view is enlarged slightly more.



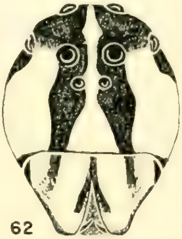
56



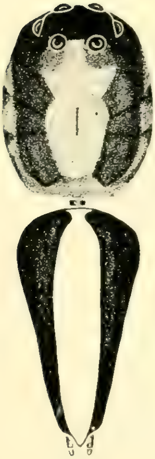
58



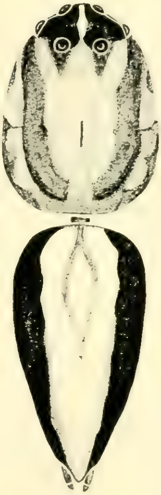
60



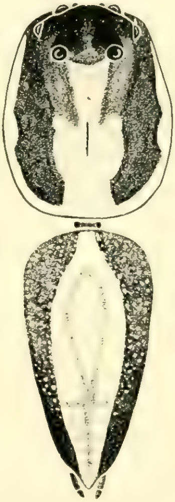
62



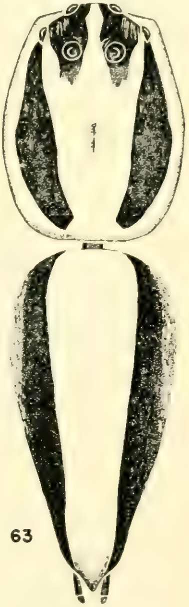
57



59



61



63

PLATE IX

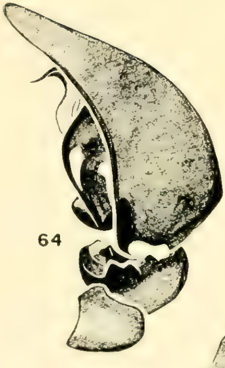
Figs. 64-65. *Oxyopes felinus* sp. n., male holotype from Molino Basin, Santa Catalina Mtns., Pima Co., Arizona, 12 July 1962. 64. Left palpus, retrolateral view. 65. Left palpus, ventral view.

Figs. 66-67. *Oxyopes lynx* sp. n., male holotype from Marathon, Brewster Co., Texas, 12 June 1948. 66. Palpus, retrolateral view. 67. Palpus, ventral view.

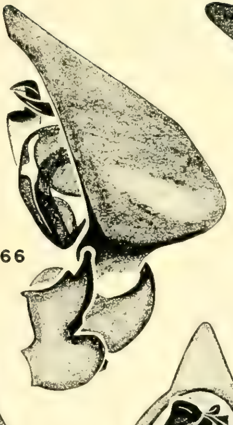
Figs. 68-69. *Oxyopes pardus* sp. n., male holotype from South Fork of Cave Creek Canyon, Chiricahua Mtns., Cochise Co., Arizona, 8 July 1962. 68. Palpus, retrolateral view. 69, Palpus, ventral view.

Figs. 70-71. *Oxyopes tridens* sp. n., male holotype from Mercury, Nye Co., Nevada, 4 July 1961. 70. Palpus, retrolateral view. 71. Palpus, ventral view.

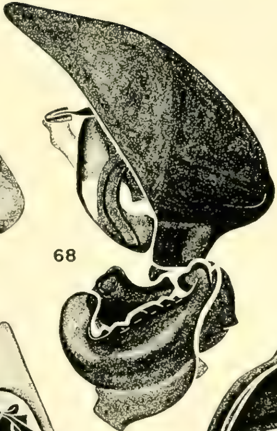
Abbreviation. P, patellar apophysis.



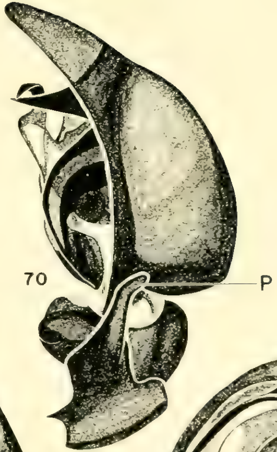
64



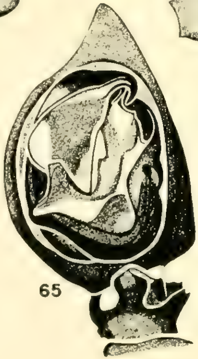
66



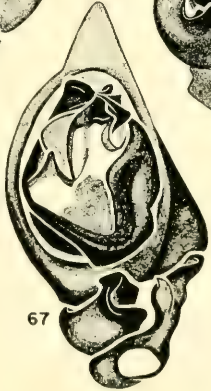
68



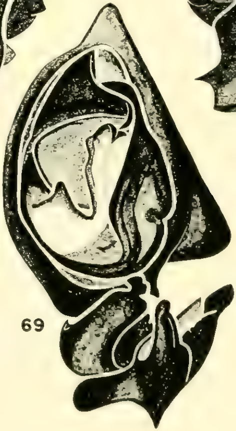
70



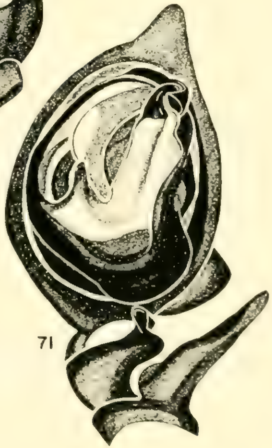
65



67



69

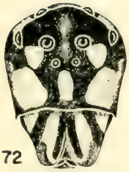


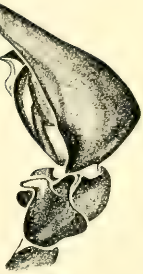
71

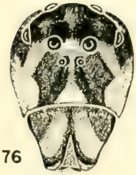
PLATE X

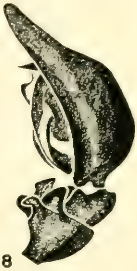
FIGS. 72-75. *Oxyopes apollo* sp. n., male holotype from Encino, Brooks Co., Texas. 72. Face view. 73. Dorsal view. 74. Left palpus, retrolateral view. 75. Left palpus, ventral view.

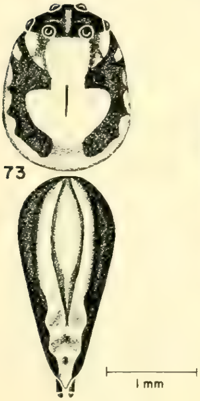
FIGS. 76-79. *Oxyopes floridanus*, male holotype from Duval Co., Florida, 17 Apr. 1949. 76. Face view. 77. Dorsal view. 78. Palpus, retrolateral view. 79. Palpus, ventral view.

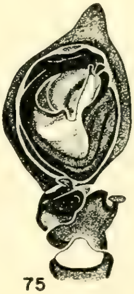

72

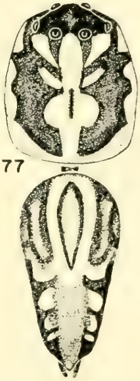

74


76


78


73


75


77

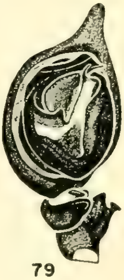

79

PLATE XI

Figs. 80-86. *Oxyopes salticus* Hentz. 80. Face view of male from Plumerville, Conway Co., Arkansas, 20 June 1957. 81-82. Male from Kingman Co. St. Pk., Kingman Co., Kansas, 14 Aug. 1962. 81. Face view. 82. Dorsal view. 83-84. Male from Plumerville, Conway Co., Arkansas, 20 June 1957. 83. Face view. 84. Dorsal view. 85-86. Female from Rooks Co. St. Pk., Rooks Co., Kansas, 18 Aug. 1962. 85. Face view. 86. Dorsal view.

Figs. 87-90. *Oxyopes scalaris* Hentz, from Hastings Nat. Hist. Reservation, Monterey Co., California, 30 May 1950. 87. Male, face view. 88. Male, dorsal view. 89. Female, face view. 90. Female, dorsal view.

Scale is for dorsal view only. The face view is enlarged slightly more.

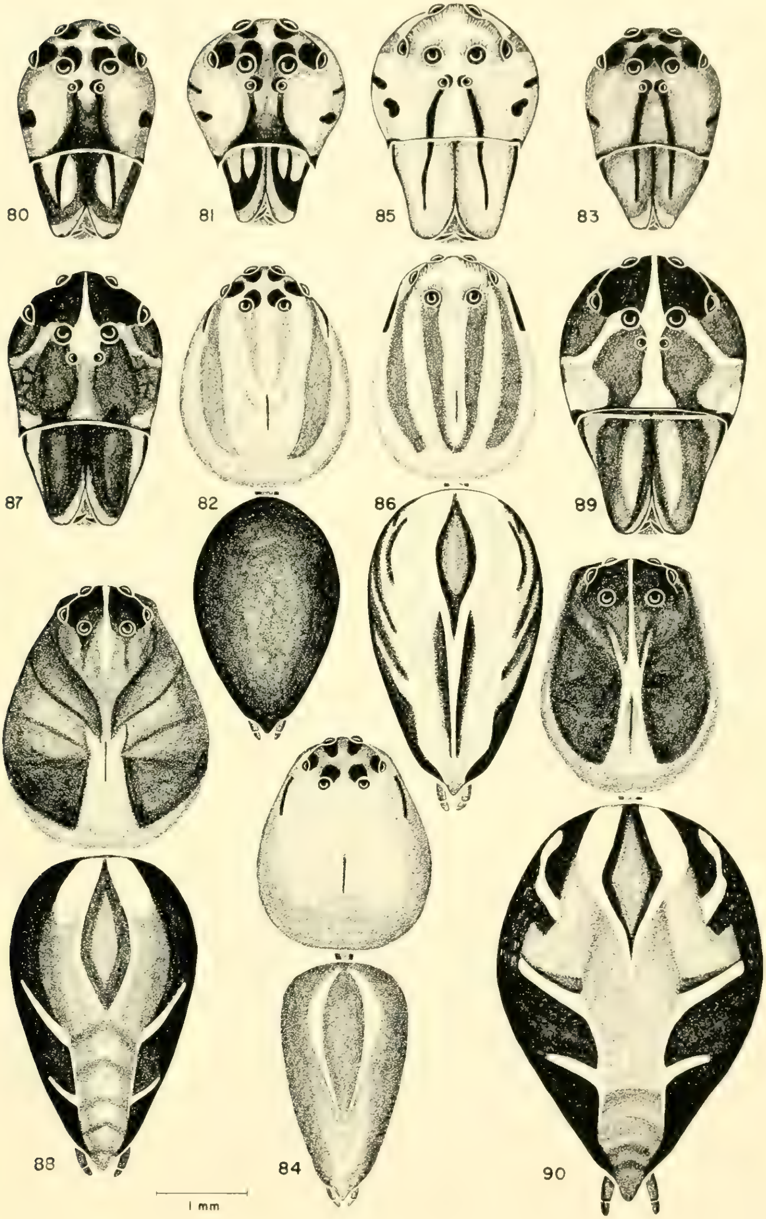

80
81
85
83
87
82
86
89
88
84
90
1 mm

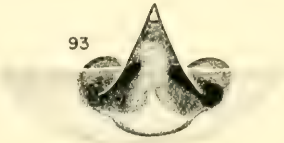
PLATE XII

Figs. 91-96. *Oxyopes salticus* Hentz. 91-92. Female from Meade Co. St. Pk., Meade Co., Kansas, 15 Aug. 1962. 91. Epigynum. 92. Internal genitalia, dorsal view. 93-96. Two females from Tracy, San Joaquin Co., California, 30 June 1938. 93. Epigynum. 94. Internal genitalia, dorsal view. 95. Epigynum. 96. Internal genitalia, dorsal view.

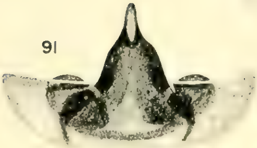
Figs. 97-99. *Oxyopes scalaris* Hentz. 97-98. Female from Hastings Nat. Hist. Rsvn., Monterey Co., California, 30 May 1950. 97. Internal genitalia, dorsal view. 98. Epigynum. 99. Epigynum of female from Ochoca Dam, 8 mi. E of Prineville, Crook Co., Oregon.

Fig. 100. *Oxyopes heterophthalmus* Latreille, epigynum of female from 4 Km S of Split, Dalmatia, Jugoslavia, 17 June 1962.

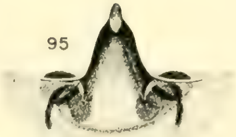
93



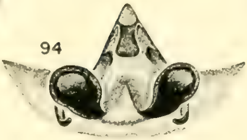
91



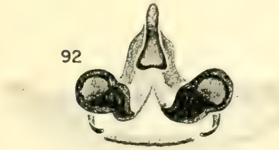
95



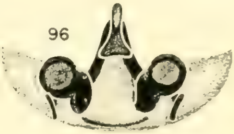
94



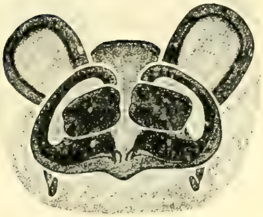
92



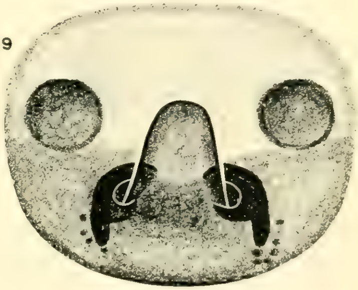
96



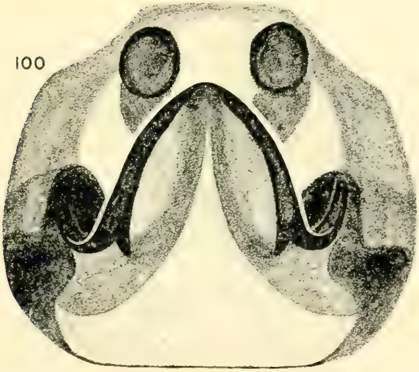
97



99



100



98

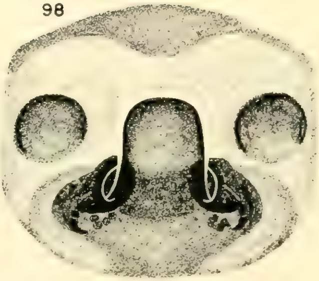


PLATE XIII

Fig. 101. *Oxyopes heterophthalmus* Latreille, retrolateral view, left palpus of male from Srebrino, Dalmatia, Jugoslavia, 13 June 1962.

Figs. 102-103. *Oxyopes gracilis* Keyserling, male from Paso Real on Rio Tonto, Oaxaca, Mexico, 29-30 July 1960. 102. Left palpus, retrolateral view. 103. Left palpus, ventral view.

Figs. 104-105. *Oxyopes salticus* Hentz, male from Kingman Co. St. Pk., Kingman Co., Kansas, 14 Aug. 1962. 104. Palpus, retrolateral view. 105. Palpus, ventral view.

Figs. 106-107. *Oxyopes scalaris* Hentz, male from Hastings Nat. Hist. Rsvn., Monterey Co., California, 30 May 1950. 106. Palpus, retrolateral view. 107. Palpus, ventral view.

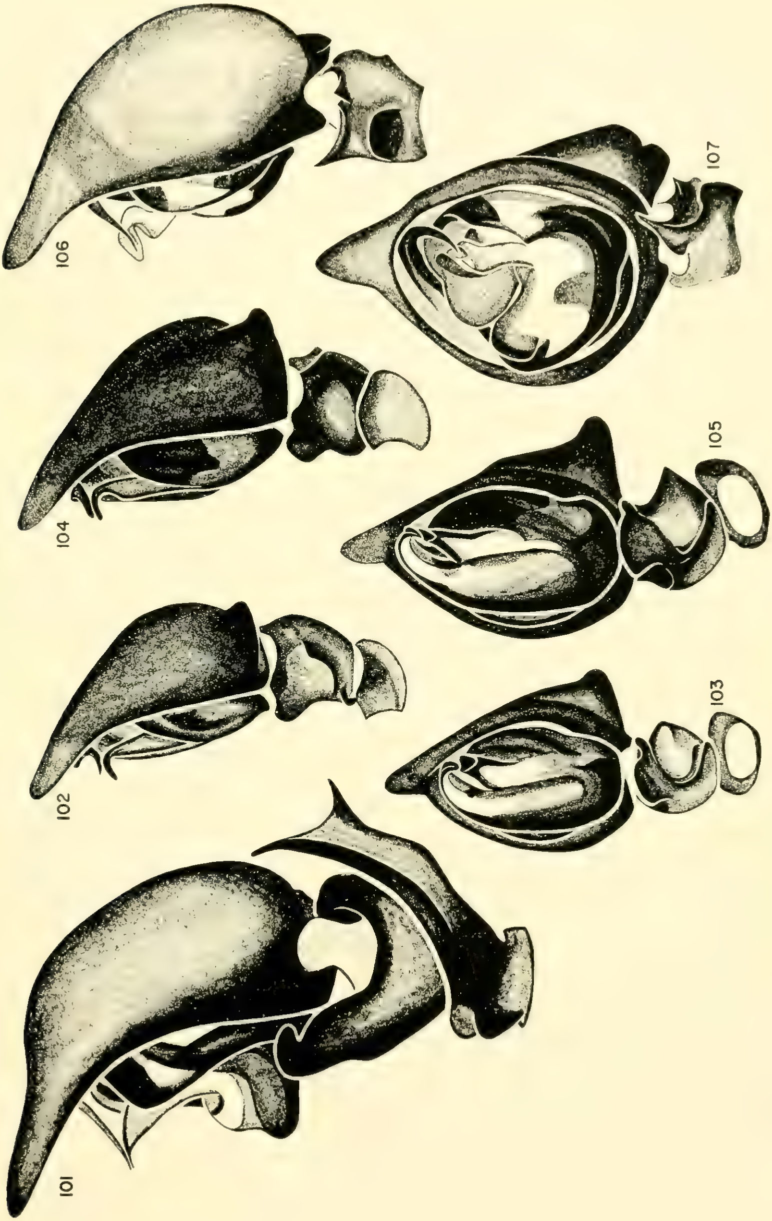


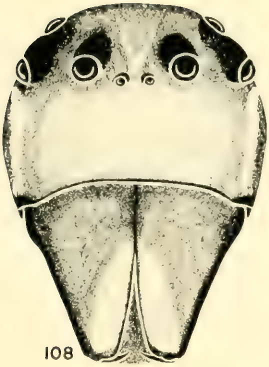
PLATE XIV

Figs. 108-109. *Hamataliwa grisea* Keyserling, female from 8 mi. SE of Rodeo, Hidalgo Co., New Mexico, 30 June 1955. 108. Face view. 109. Dorsal view.

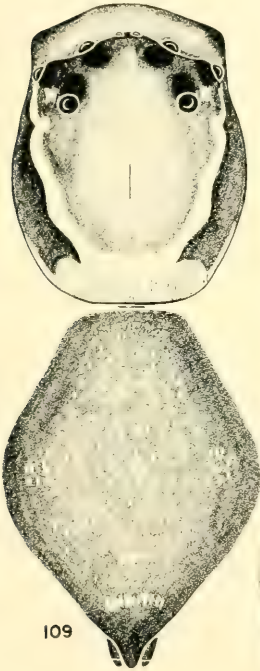
Figs. 110-111. *Hamataliwa unca* sp. n., female from Brownsville, Cameron Co., Texas, 8 June 1934. 110. Face view. 111. Dorsal view.

Figs. 112-114. *Hamataliwa helia* (Chamberlin), females from Torreya St. Pk., Liberty Co., Florida, 23 June 1962. 112. Face view. 113. Dorsal view. 114. Dorsal view.

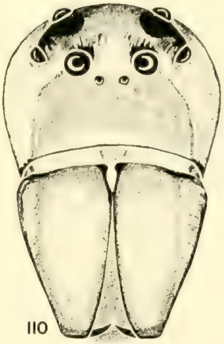
Scale is for dorsal view only. The face view is enlarged slightly more.



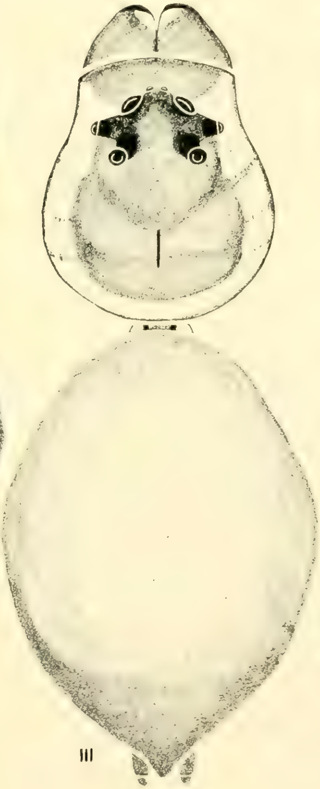
108



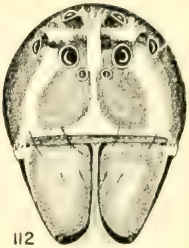
109



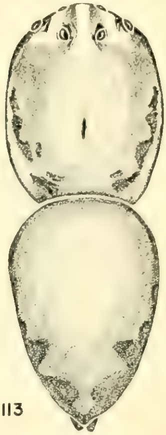
110



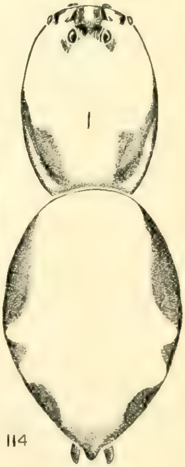
111



112



113



114

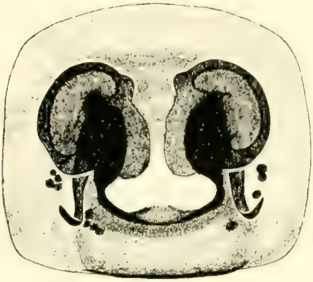
1 mm

PLATE XV

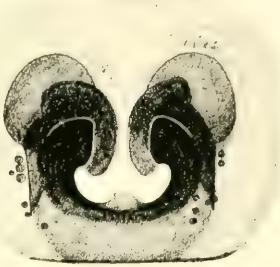
Figs. 115-116. *Hamataliwa grisea* Keyserling, female from 8 mi. SE of Rodeo, Hidalgo Co., New Mexico, 30 June 1955. 115. Internal genitalia, dorsal view. 116. Epigynum.

Figs. 117-118. *Hamataliwa unca* sp. n., female from Brownsville, Cameron Co., Texas, 8 June 1934. 117. Internal genitalia, dorsal view. 118. Epigynum.

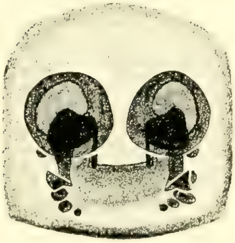
Figs. 119-121. *Hamataliwa helia* (Chamberlin), female from Torreya St. Pk., Liberty Co., Florida, 23 June 1962. 119. Internal genitalia, dorsal view. 120. Epigynum. 121. Left leg I, prolateral view.



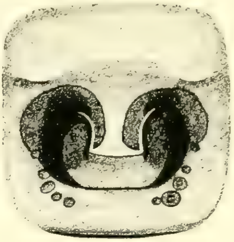
115



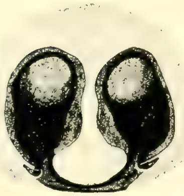
116



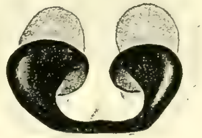
117



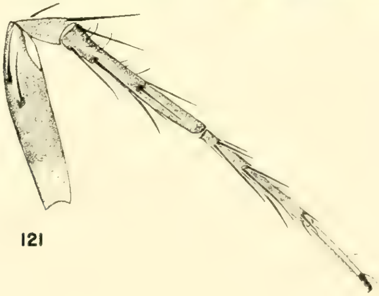
118



119



120



121

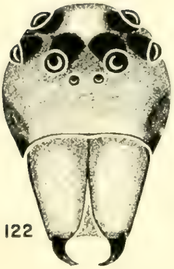
PLATE XVI

FIGS. 122-123. *Hamataliwa unca* sp. n., male holotype from Edinburg, Hidalgo Co., Texas, Sept.-Dec. 1933. 122. Face view. 123. Dorsal view.

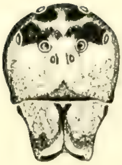
FIGS. 124-125. *Hamataliwa helia* (Chamberlin), male from Torreya St. Pk., Liberty Co., Florida, 23 June 1962. 124. Face view. 125. Dorsal view.

FIGS. 126-127. *Hamataliwa grisea* Keyserling, male from 8 mi. SE of Rodeo, Hidalgo Co., New Mexico, 30 June 1955. 126. Face view. 127. Dorsal view.

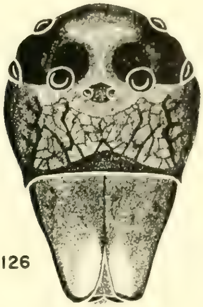
Scale is for dorsal view only. The face view is enlarged slightly more.



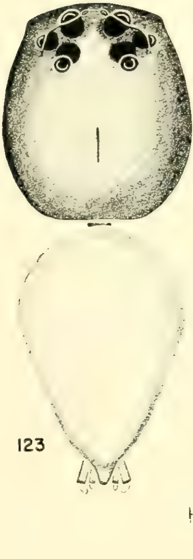
122



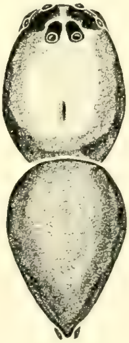
124



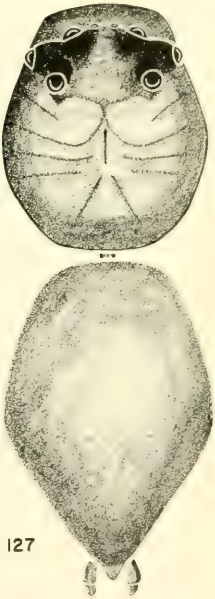
126



123



125



127

1 mm

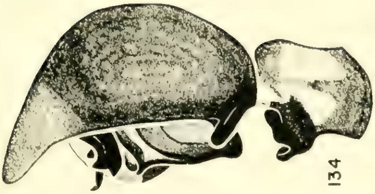
PLATE XVII

FIGS. 128-129. *Hamataliwa unca* sp. n., male holotype from Edinburg, Hidalgo Co., Texas, Sept.-Dec., 1933. 128. Left palpus, retrolateral view. 129. Left palpus, ventral view.

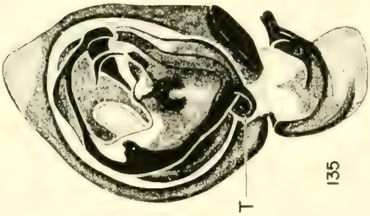
FIGS. 130-133. *Hamataliwa helia* (Chamberlin), males from Torreya St. Pk., Liberty Co., Florida, 23 June 1962. 130. Palpus, retrolateral view, tip of embolus not resting on conductor. 131. Palpus, ventral view, embolus not resting on conductor. 132. Palpus, retrolateral view, tip of embolus resting normally against conductor. 133. Palpus, ventral view, tip of embolus resting normally against conductor.

FIGS. 134-135. *Hamataliwa grisea* Keyserling, male from 8 mi. SE of Rodeo, Hidalgo Co., New Mexico, 30 June 1955. 134. Palpus, retrolateral view. 135. Palpus, ventral view.

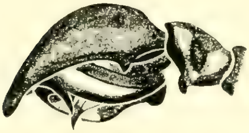
Abbreviation. T, twist of embolus.



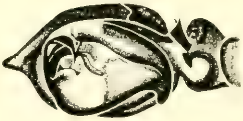
134



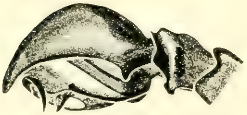
135



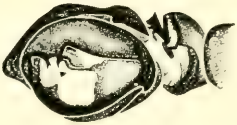
132



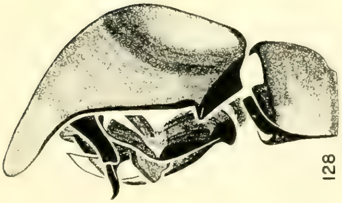
133



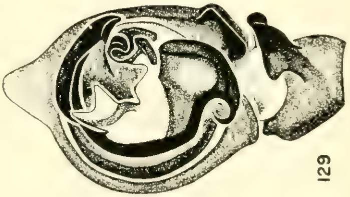
130



131



128



129

PLATE XVIII

FIGS. 136-139. *Peucetia viridans* (Hentz), female from Rancho El Mirador, Baboquivari Mtns., Pima Co., Arizona, 4 Sept. 1950. 136. Face view. 137. Dorsal view. 138. Right leg I, prolateral view. 139. Labium, endites and sternum, ventral view. 140. Face view of female from Gainesville, Alachua Co., Florida, 6 Nov. 1936. 141-142. Male from Rancho El Mirador, Baboquivari Mtns., Pima Co., Arizona, 4 Sept. 1950. 141. Face view. 142. Dorsal view.

Scale is for dorsal view and leg. Face, labium, endites and sternum are enlarged slightly more.

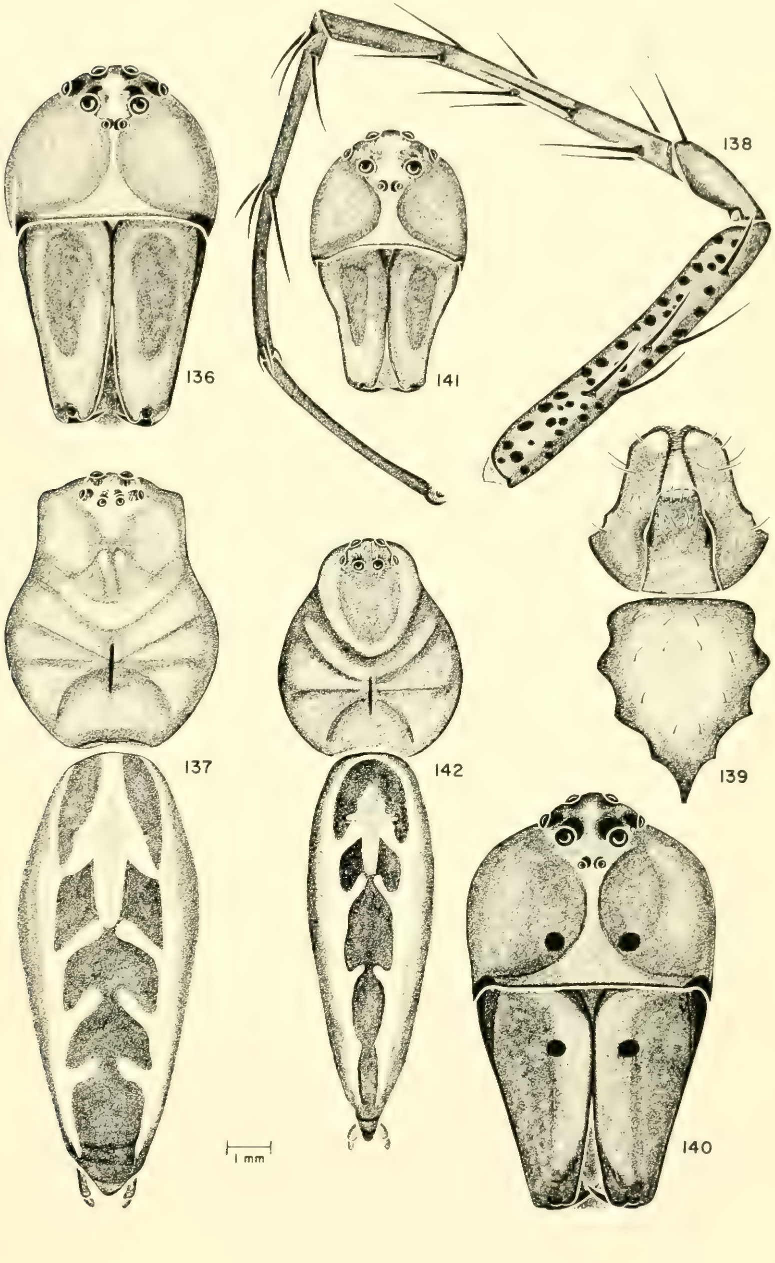
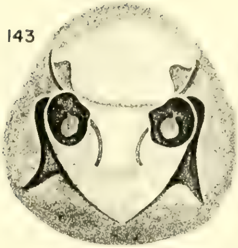

1 mm

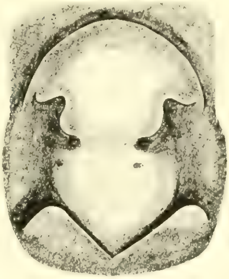
PLATE XIX

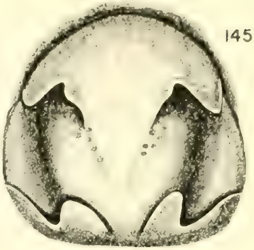
Figs. 143-148. *Peucetia viridans* (Hentz). 143-144. Female from Gainesville, Alachua Co., Florida, 6 Nov. 1936. 143. Internal genitalia, dorsal view. 144. Epigynum. 145. Epigynum of female from Rancho El Mirador, Baboquivari Mtns., Pima Co., Arizona, 4 Sept. 1950. 146-147. Female from Brown's Canyon, Baboquivari Mtns., Pima Co., Arizona, July 1952. 146. Internal genitalia, dorsal view. 147. Epigynum. 148. Epigynum of female from Kennard's Prairie near Marquez, Leon Co., Texas, 26 Oct. 1958.

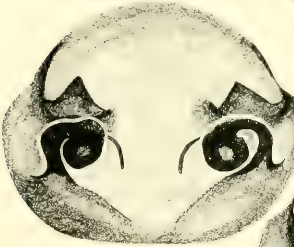
Figs. 149-150. *Peucetia bibranchiata* F. O. P.-Cambridge, female from Veracruz, Veracruz, Mexico. 149. Internal genitalia, dorsal view. 150. Epigynum.

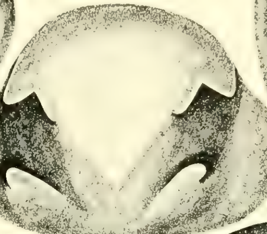
Figs. 151-153. *Peucetia longipalpis* F. O. P.-Cambridge. 151-152. Female from Harlingen, Cameron Co., Texas. 151. Internal genitalia, dorsal view. 152. Epigynum. 153. Epigynum of female from Brown's Canyon, Baboquivari Mtns., Pima Co., Arizona, 9 June 1952.

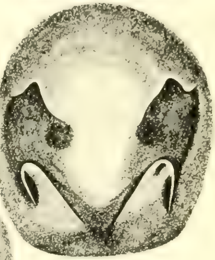

143

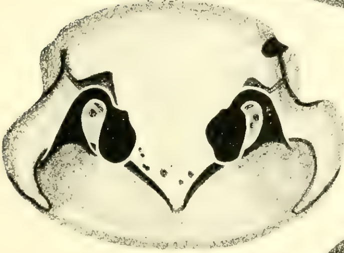

144

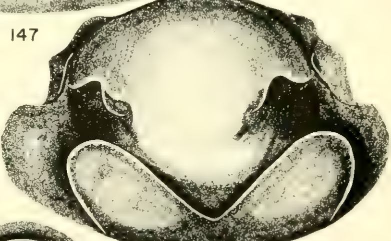

145

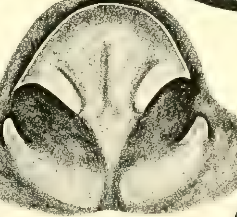

146


147

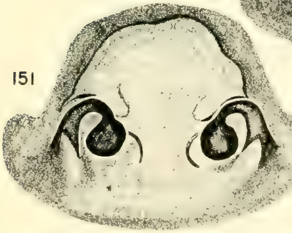

148


149


150


152

0.5 mm


151

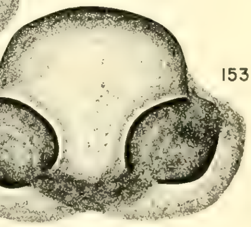

153

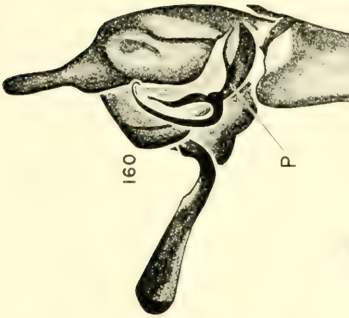
PLATE XX

Figs. 154-155. *Peucetia longipalpis* F. O. P.-Cambridge, male from Brown's Canyon, Baboquivari Mtns., Pima Co., Arizona, 9 June 1952. 154. Left palpus, retrolateral view. 155. Left palpus, ventral view.

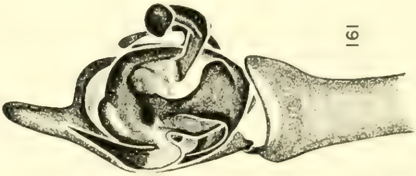
Figs. 156-157. *Peucetia bibranchiata* F. O. P.-Cambridge, male from Costa Rica. 156. Palpus, retrolateral view. 157. Palpus, ventral view.

Figs. 158-161. *Peucetia viridans* (Hentz). 158-159. Male from Silverhill, Baldwin Co., Alabama, Sept. 1945. 158. Palpus, retrolateral view. 159. Palpus, ventral view. 160-161. Male from Madera Canyon, Santa Rita Mtns., Pima Co., Arizona, 25 Aug. 1950. 160. Palpus, retrolateral view. 161. Palpus, ventral view.

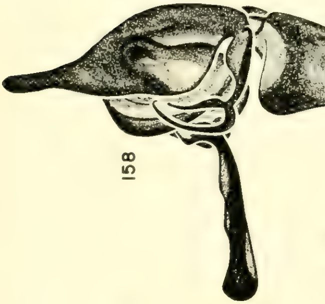
Abbreviation. P, paracymbium.



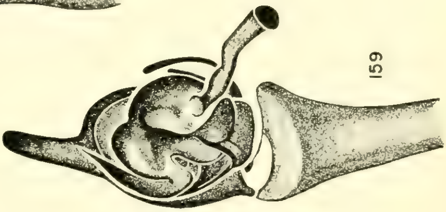
160



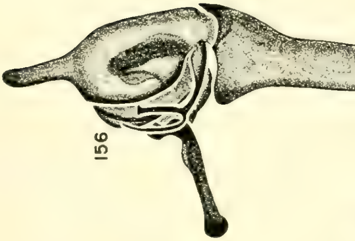
161



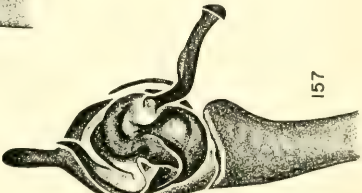
158



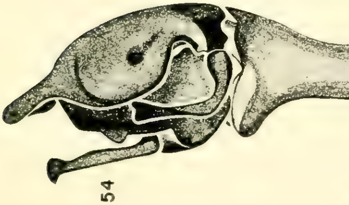
159



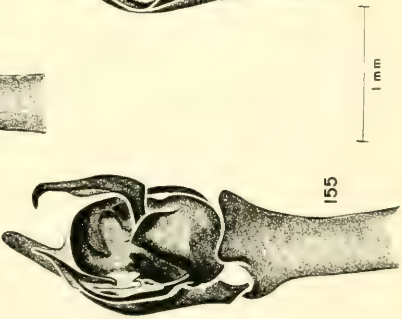
156



157



154



155

Harvard MCZ Library
3 2044 066 304 007